EFFECTS OF PHYSICAL DISTURBANCE ON PHYTOPLANKTON DIVERSITY AND COMMUNITY COMPOSITION IN GALVESTON BAY, TX, DURING AN EXTREME FLOODING EVENT

A Thesis

by

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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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May 2017

Major Subject: Oceanography

ABSTRACT

With climate change, future storm frequencies and intensities and El Niño events are expected to increase. These have the potential to cause flooding within the Galveston Bay (Texas) watershed as well as other locations. Increased rainfall can lead to changes in phytoplankton diversity, biomass and density in estuarine communities and cause phytoplankton community composition shifts. However, studies showing the specific physical drivers of these community composition changes are limited. In the spring of 2015, areas within the Galveston Bay watershed experienced extreme rainfall that caused this bay to receive unusually large amounts of freshwater inputs that lead to flooding. Wind speed, mean daily freshwater inflows, mean daily tide height and individual water quality parameters such as salinity, temperature, and dissolved oxygen were collected in order to examine their effects on phytoplankton diversity and community composition. Daily water samples were taken from lower Galveston Bay (29.31 N, -97.21 W) adjacent to the Gulf of Mexico. The phytoplankton in these samples were examined using an Imaging FlowCytobot in order to document community composition shifts down to lowest practical identification level. Temperature, freshwater inflows and salinity were the major physical drivers of phytoplankton community composition in Galveston Bay over the study period. In addition, during the flooding event, phytoplankton diversity, biovolume and abundance decreased. This event also corresponded with a decrease in dinoflagellate abundance and an increase in diatom abundance. It was found that during the transition between the flooding and end of the

flooding event there was an increase in *Myrionecta* sp., suggesting an important predator- prey relationship after extreme floods in this system. The pre-flooding and post-flooding phytoplankton communities were primarily driven by temperature, indicating that they were more influenced by seasonal changes than the flooding event. Compared to previous studies, this approach has allowed us to link much finer scale community composition changes in Southern Galveston Bay, both temporally, through daily sampling, and taxonomically, through genus level taxonomic resolution, with physical parameters. This will be the first study looking at the effects of tide height and wind speed on phytoplankton in Galveston Bay. These novel results can help researchers have a better idea of how the physical changes that come with climate change can affect the base of the marine trophic web.

DEDICATION

This thesis is dedicated to the members of the Phytoplankton Dynamics Laboratory and their fearless leader, Dr. Antonietta Quigg.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Antonietta Quigg, and my committee members, Dr. Anna Armitage, Dr. Daniel Roelke and Dr. Gilbert Rowe for their support throughout my degree.

To Texas Parks and Wildlife, for providing the funding for this project, and to all of my past and present colleagues in the Phytoplankton Dynamics Laboratory at Texas A&M University at Galveston. In addition, I would like to extend thanks to collaborators and Woods Hole Oceanographic Institution; Heidi Sosik, Joe Futrelle, and Emily Peacock for their invaluable training on IFCB methods.

Finally, thank you to my husband, mother and Marissa Borrego for their undying support, love and patience.

CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supervised by a thesis committee consisting of Professor Antonietta Quigg – advisor, Daniel Roelke, and Gilbert Rowe of the Department of the Department of Oceanography and Professor Anna Armitage of the Department of Marine Biology.

Wind speed and tide height data were provided by NOAA. The daily IFCB data was collected in part by Sharon Lawrence, an undergraduate student at Texas A&M University at Galveston, Jennifer Genzer, a graduate student at Texas A&M University at Galveston and Jamie Steichen, a postdoctoral researcher at Texas A&M University at Galveston. Galveston Bay salinity maps were created by Rachel Windham, the manager of the Phytoplankton Dynamic Laboratory at Texas A&M University at Galveston. The creation of code that allowed for the efficient analysis of IFCB data was done in Heidi Sosik's Lab at Woods Hole Oceanographic Institution.

All other work conducted for the thesis was completed by the student independently.

Funding Sources

Graduate study was supported by the Doctoral Diversity Fellowship from Texas A&M University and Texas Parks and Wildlife. This work was made possible by Texas Parks and Wildlife Department #802 (TPWD sponsor award # 475858 and 428577) and Texas Commission on Environmental Quality (TCEQ sponsor award # 582-16-60152) through Texas A&M Agrilife Research.

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1. INTRODUCTION

Globally, phytoplankton are extremely important. Inside the marine and freshwater photic zones, they are responsible for 50 percent of the world's primary productivity (Longhurst, Sathyendranath, Platt, & Caverhill, 1995). Phytoplankton are remarkably diverse and differ in their evolution and distribution (Falkowski et al., 2004). Recent estimates suggest that there may be nearly 200,000 species of diatoms alone (Armbrust, 2009). The majority of ocean species are yet to be discovered (Mora, Tittensor, Adl, Simpson, & Worm, 2011). Across latitudes, phytoplankton diversity is lowest at the poles and increases toward the equator. This excludes hot spots such as upwelling areas (Barton, Dutkiewicz, Flierl, Bragg, & Follows, 2010). Generally speaking, at low biomass (~2 mg C m^{-3}), nanophytoplankton and picophytoplankton are co-dominant. When biomass is high (~100-300 mg C m^{-3}), large species are usually dominant, while very high biomass (1,000 mg C m^{-3}) usually indicates domination by one species, likely due to a phytoplankton bloom (Irigoien, Huisman, & Harris, 2004). Maximum diversity generally occurs at intermediate phytoplankton biomass (Irigoien et al., 2004).

There is potential for diversity to be used as a bio-indicator of stability and ecosystem "health". If, over time, a system maintains a high and stable diversity index, this can be used as an indicator of high resource use efficiency and steady functions in the system because resource use efficiency and community composition are stabilized by diversity (Corcoran & Boeing, 2012; Ives & Carpenter, 2007; McCann, 2000; Tilman,

1999). In contrast, decreased diversity can indicate monospecific blooms in which there is high density of one or a few species. The frequency of this could potentially be used as an indicator of poor system "health" and/or eutrophication (Cooper & Brush, 1991; J. L. Pinckney, Quigg, & Roelke, 2016). Low diversity can also indicate competitive exclusion due to a less dynamic system and large changes in diversity can indicate stress in a system. Therefore, persistence of high diversity could signal less harmful algal blooms (HABs) and eutrophication which is important in maintaining productive systems that can lead to more profitable fisheries and revenue from recreation.

Near shore systems such as estuaries (characterized by the presence of rivers meeting a marine environment) are one of the most chemically and physically heterogeneous marine environments (Yamamoto & Hatta, 2004). In a highly variable environment, the relationships between the communities and their surroundings are much more complex compared to the open ocean. This is largely due to processes associated with land, sediments, the ocean and the atmosphere (J. E. Cloern, 1996). In contrast, in the open ocean, phytoplankton community composition variability is explained predominately by yearly solar and heat cycles (Cushing, 1959; Mutshinda, Finkel, Widdicombe, & Irwin, 2016; Sverdrup, 1953).

Rivers bring nutrients, sediments, and lower salinities to an estuary through freshwater inflows (FWIs). This is important because phytoplankton abundance, biomass, diversity, size structure and the types of taxa present are known to change with alterations in the environment (Nixon, 1995; H. W. Paerl, Valdes-Weaver, Joyner, & Winkelmann, 2007). Local processes that effect the diversity of phytoplankton are

spatial & temporal heterogeneity, grazing/keystone predators (Leibold, 1996), chaos (Benincà et al., 2008; Dakos et al., 2009), light (Stomp et al., 2004) and sizes of resources (Yoshiyama & Klausmeier, 2008). This study will focus on the effects of heterogeneity in the form of physical disturbance.

With climate change, we have observed and are experiencing a greater frequency of disturbance events such as drought and flood (Bender et al., 2010; Goldenberg, Landsea, Mestas-Nuñez, & Gray, 2001). In a number of cases, these are also what may be considered extreme events. For example, from October 2010 to December 2011, Texas experienced such a significant and prolonged drought that 88 percent of the state was declared to be under exceptional drought conditions (Nielsen-Gammon, 2012). This event was the most intense one-year drought since state records began in 1895 (Nielsen-Gammon, 2012).

Extreme flood events have caused substantial alterations to estuaries. For example, three hurricanes struck Pamlico Sound in North Carolina in the fall of 1999 and caused large ecological changes to the lagoon. These changes included hypoxic bottom waters associated with a tripling in phytoplankton biomass that had adverse effects at higher trophic levels (Adams, Greeley, Law, Noga, & Zelikoff, 2003; H. W. Paerl et al., 2001; Tester et al., 2003). However, in Chesapeake Bay, extreme FWIs due to hurricanes produced lower residence times (1-3 wk.) which reduced overall phytoplankton biomass and caused an increase in diatom abundance (H. W. Paerl, Valdes, Peierls, Adolf, & Harding Jr, 2006). Diatoms were likely favored due to their high growth rates and nutrient storage capacities (Malone, Crocker, Pike, & Wendler,

1988; J. L. Pinckney, Paerl, & Harrington, 1999). Disturbance due to extreme flooding and drought may lead to lasting alterations to estuarine productivity and community composition that could lead to changes up the trophic ladder (Adams et al., 2003; H. W. Paerl et al., 2001).

Galveston Bay, Texas, the location for this study, is a commercially important estuary that produces more than $1 billion annually from fisheries production (Lester & Gonzalez, 2011). However, this bay also houses many harmful phytoplankton species, experiences intermittent blooms, has a growing human population within its watershed, and has had a high potential for the introduction of non-native species (Örnólfsdóttir, Lumsden, & Pinckney, 2004a). This makes it especially important to understand how physical properties can mitigate or aggravate these known issues.

This work was performed just before to just after the extreme flooding event of spring-summer 2015 (4/2/15-7/31/15). During this period, in an approximately two-month time frame, enough rain fell in order to cover the entire state of Texas in over a foot of water and likely greatly increased the amount of FWIs and energy coming into this system over this time. In order to examine the effects of this flood event, it will be necessary to describe how the mean daily tides, mean daily FWIs, wind speed and other environmental variables influence phytoplankton diversity in Galveston Bay. The purpose of this study is to determine the effects of physical disturbance on phytoplankton diversity and community composition in Galveston Bay, Texas.

2. HYPOTHESIS

Strong physical disturbance, including an extreme flooding event in Galveston Bay, will lead to a shift in phytoplankton community composition from slower growing taxa to faster growing taxa and will decrease phytoplankton diversity.

3. METHODS

3.1 Study Site

Samples were taken from a time-series station in Galveston Bay (Figure 1). This bay is the second largest estuary in the Gulf of Mexico and the seventh largest in the United States (area of 1,554 km^2). It is a shallow estuary (average 2-3 m depth) with a shipping channel (15 m deep & 200 m wide) that runs from the entrance to the Gulf of Mexico to Buffalo Bayou, near the mouth of the San Jacinto River. Seawater enters Galveston Bay through this ship channel and freshwater leaves along the eastern side (Powell, Klinck, Hofmann, & McManus, 2003). FWI enters from the Trinity River (55%), the San Jacinto River and Buffalo Bayou (26%), and tributaries located around the bay (Guthrie et al., 2012). Galveston Bay has a low (0.15 m) tidal range consisting of mostly diurnal micro-tides with semidiurnal tides during neap periods (Rayson, Gross, & Fringer, 2015). Depth averaged tidal velocity at NOAA's Galveston Bay (GB) Entrance station (ID # 8771341) peaks at 0.8-0.9 m s^{-1} (Rayson et al., 2015). Tidal and low frequency water levels vary 1 m with a 3-10 day period variability in water level (Rayson et al., 2015). Water level variation is greatest from September-June with a maximum in October and minimum in February (Rayson et al., 2015). In this system, diurnal tides account for 50 percent of water level variance while the other 50 percent is accounted for by coastal winds. Tidal currents are ~3 times larger than subtidal currents at the bay's entrance (0.9 ms^{-1} vs 0.3). Subtidal currents are forced by wind-driven water level changes (Rayson et al., 2015).

As measured previously (1985-86), the average salinity was 5-10 psu lower from April-June than from August-October and salinity variability in this system is mainly driven by the Trinity River (Orlando, 1993; Rayson et al., 2015). Seasonal (2007-2012) discharge patterns from the Trinity River were as follows: from February-March river discharge was from 300-375 m^3s^{-1}, it was the lowest from August-September where the average was 100 m^3s^{-1}, while peak discharge was > 1000 m^3s^{-1} (Rayson et al., 2015). May and immediately before usually had highest FWI into Galveston Bay (Longley, 1994; J. Pinckney, 2006).This is especially important because changes in temperature and FWIs (magnitude, duration) are the major causes of phytoplankton community changes in Galveston Bay (Dorado et al., 2015; D. L. Roelke et al., 2013). However, the salinity near the entrance is more variable than near the rivers. This means that processes other than FWI are responsible for the salinity, and possibly the phytoplankton community, at this location (Rayson et al., 2015).

The effects of mean daily tide height on Galveston Bay phytoplankton were analyzed using data from NOAA's Tides and Currents daily tide height prediction from the Pier 21 station (ID: 8771450) located near the daily sampling station (Figure 1). https://tidesandcurrents.noaa.gov/noaatidepredictions/NOAATidesFacade.jsp?Stationid=8771450 . In the past (Dorado et al., 2015; Örnólfsdóttir et al., 2004a), studies in Galveston Bay have ignored tides as possible drivers of phytoplankton community composition due to their micro-tidal nature. This reasoning makes sense for bay wide studies, but for a station near the mouth of the bay, it is important to take tidal variations into account in order to find if the changes in salinity and the merging of water types can

change community composition. This is especially important because HAB species often enter into the bay through this opening (Hetland & Campbell, 2007).

Wind speed was analyzed as a possible driver of community composition variability during an extreme flooding event using data from NOAA's Galveston Bay Entrance station (ID: 8771341) https://tidesandcurrents.noaa.gov/ports/ports.html?id=8771341&mode=show_all due to a lack of wind data from the Pier 21 station (Figure 1). Phytoplankton sampling in Galveston Bay has largely been conducted from small vessels. Therefore, there are no studies in Galveston Bay showing the effects of wind on phytoplankton community composition due to the bias associated with safe boating days. Because Galveston Bay is largely a wind mixed system, with the most dominant wind coming from the Southeast (Park, Wade, & Sweet, 2001), it is important to understand the effects of wind on this system.

The sampling location for this study is on the shoreline of Pelican Island (29.31 N, -97.21 W) in Galveston Bay near the bay's entrance to the Gulf of Mexico. This station is primarily used to monitor for HAB species on a daily basis and was selected because, as mentioned above, harmful algal species along the Texas coast tend to wash in from offshore. Imaging FlowCytobot (IFCB), the instrument used in this study, has been successfully used as an early warning system for HABs in Port Aransas on the Texas coast (L. Campbell et al., 2010).

3.2 Imaging FlowCytobot (IFCB)

IFCB (Figure 2) is a cutting edge instrument that combines imaging and flow cytometry in order to take high resolution images of particles in a size range of ~10-100 µm (Olson & Sosik, 2007; Sosik & Olson, 2007). In order to capture these images, a field sample is passed through a 130 µm nylon mesh intake in order to restrict large particles that could clog the fluidics from entering into the system (Figure 3). The sample is inserted into the center of the flow cell via a clean, smoothly flowing sheath fluid made of filtered seawater that has been pushed through two 0.2 µm filter cartridges. This sheath fluid moves the cells one by one across a laser beam and then into the imaging field of view of the camera. This laminar flow ensures that all particles are in focus and that each cell is more likely to be imaged individually (Olson & Sosik, 2007). Once the cell passes through the 4.5 mW red diode laser, the chlorophyll containing particles (such as phytoplankton) scatter light and emit a red (680 nm) fluorescence. This fluorescence triggers a xenon flash lamp that illuminates the flow cell and allows for image acquisition. 6 µm internal standard bead samples were run periodically in order to monitor instrument performance. This instrument is superior to a similar machine, the FlowCam (Sieracki et al, 1998), in that the IFCB can capture better resolution (~1 µm) images and has the ability to be deployed in situ for months at a time. The IFCB can image a 5 ml sample in ~20 minutes. Therefore, it is an efficient method to view the individual cells in order to identify them down to genus level.

This efficiency is what separates this method from earlier protocols. In the past, phytoplankton community composition has most commonly been measured using

microscopy and High Performance Liquid Chromatography (Heukelem, Lewitus, Kana, & Craft, 1992; Millie, Paerl, & Hurley, 1993). While studies using these methods have been largely successful, it is difficult to obtain both fine scale temporal and taxonomic data. These methods are time consuming and can be expensive. There are very few trained taxonomists which are skillful with a microscope. The IFCB allows researchers to calculate more accurate diversity measurements and find trends in phytoplankton diversity that would be undiscoverable with the level of taxa available from phytoplankton pigments alone (J. L. Pinckney et al., 2016).

Daily water samples and environmental measurements were taken from the time-series station. Each day between 0900 and 1000, a pitcher was rinsed three times with sample water and used to rinse an acid washed, brown, 1L bottle three times and fill it with a water sample. Sampling occurred daily because it is known that large changes in community can occur over a time scale of days (Cesar & Abreu, 2009; Jassby & Van Nieuwenhuyse, 2005). A calibrated (once per month) MS5 Hydrolab was used to collect environmental data (Dissolved Oxygen, temperature, Salinity and Specific Conductivity) at the same time as each daily sample. IFCB samples were run immediately after collection, using 5 ml at a time. Sampling was continued until 200 cells were counted.

The imaged cells were identified to genus level (when possible) and enumerated. Identifications were done visually using several phytoplankton identification references (Al-Kandari, Al-Yamani, & Al-Rifaie, 2009; P. Campbell, 1973; Hoppenrath, Elbrächter, & Drebes, 2009; Horner, 2002; Kraberg, Baumann, & Dürselen, 2010; Tomas, 1997). Cells that could not be identified to genus level were given descriptive

names such as “Sigmoid Pennates”, “Pennate Diatoms”, “Rod like Diatoms”, “Flagellate Mix” (Flagellated cells with no cingulum/not dinoflagellates), “Cell Mix” (Unidentifiable cells with no flagella, no cingulum) and “Unidentified Dinoflagellates (flagellated cells with a cingulum)”. The resulting abundance, biovolume and physical data were then utilized in examining the effects of the 2015 extreme flooding event on the phytoplankton community using the following methods.

The autotrophic ciliate *Myrionecta sp.* was included in this study because it is an obligate autotroph and it has been shown to retain multiple plastids for up to 30 days (Johnson, Oldach, Delwiche, & Stoecker, 2007). This means that it is likely that these cells had an equal chance of being imaged as the phytoplankton. In addition, this genera was numerically important over this study period and has the potential to cause red tides, similar to many phytoplankton (Johnson, Tengs, Oldach, & Stoecker, 2006).

In addition to abundance data, cell biovolumes were calculated for each genus using distance maps (Moberg & Sosik, 2012). In this method, an outline is drawn around the boundaries of the cells. Next, the distance of each interior pixel from the boundary is calculated (Figure 4). These distances are used to project the pixels into 3D space. The volume derived from this is then corrected for by a multiplicative factor that assumes locally circular cross-sections. This method is best for IFCB sampling because it is a computationally efficient method that is unbiased, accurate and comparable to traditional microscopic methods for a range of cell morphologies (Moberg & Sosik, 2012). A MATLAB script was prepared for use by Heidi M. Sosik at Woods Hole Oceanographic Institution and shared with our lab to use on these samples.

3.3 Comparing FWIs of 205 Flooding Event to a Neutral Year

In order to visualize the extreme FWI event of 2015, discharge data was collected from the USGS Romayor station for 2014, a neutral year, and 2015, the flood year. This discharge data was plotted for each year from April-July. It was also averaged over each flooding stage for both years in order to compare the differences in freshwater discharge from the Trinity River between the neutral and flooding years.

Salinity maps from both years were interpolated using the mapping software, Surfer, utilizing data from the Galveston Bay Project's monthly water quality monitoring efforts. This data was collected by a continuous data logger, called a Dataflow, which measures water quality parameters once every second from a moving vessel traveling over a sampling transect.

3.4 Galveston Bay Water Quality/ Physical Parameters

Water quality (Temperature, Dissolved Oxygen, Salinity) and physical (wind speed, and mean daily tide height) parameters were plotted over the study period in order to determine statistically significant linear trends, and in order to observe patterns that may have occurred due to the extreme FWI event.

3.5 Defining the Flood Stage Timeline

River flows measured by the United States Geological Survey (USGS) gage at the Romayor (Station # 08066500) were used to determine the discharge rates of water flowing into Galveston Bay from the Trinity River. In order to better interpret the effects of the flood on phytoplankton community composition and diversity, it is essential to know when the flooding event began and how long it lasted. A hierarchical

agglomerative cluster analysis with group-average linking on the Euclidean distances between all environmental parameters (Temperature, Salinity, Dissolved Oxygen, Mean Daily Tide Height, Wind Speed, and Mean Daily FWIs) was run over all days of the sampling period. This coupled with freshwater discharge values allowed for the determination of the three flood stages; pre-flood, flood and post-flood. A Similarity Profile (SIMPROF) test of 9999 permutations and a significance level of 5% was run in conjunction with the cluster analysis, which allows for statistical robustness.

3.6 Calculating Phytoplankton Community Diversity

In this study, Simpson's inverse index (1-ʎ)' was calculated on phytoplankton cell densities in order to assess the degree of variation of genera in each sample. Simpson's index works well with small sample sizes and consistently ranks assemblages (A. Magurran, 2004). Simpson's Index also performs well under the six criteria of Buckland et al. (2005) which suggests criteria that a diversity index should generally measure (Buckland, Magurran, Green, & Fewster, 2005; A. E. Magurran & McGill, 2011). However, it can fail if all species are declining at the same rate, because the index will stay constant (A. E. Magurran & McGill, 2011). Although Shannon Diversity is generally popular in phytoplankton studies, it is not the best choice because interpretation can be difficult, and as rare species become present in large proportions of the abundance, the diversity can be a function of sample size (Lande, Engen, & Saether, 2003; A. Magurran, 2004; A. E. Magurran & McGill, 2011).

3.7 Community Composition Changes

In order to provide an idea of the community as a whole, total cell abundance and biovolume for each sample was calculated and plotted. Linear regression analyses were utilized in order to determine the significance of these patterns.

One way Analysis of Similarities (ANOSIMs) with 9999 permutations on the Euclidean distances of all the environmental data and Bray-Curtis similarities of the phytoplankton abundance data were calculated in order to examine if there were differences between the environmental and phytoplankton community composition data during the three flooding stages.

In order to visualize community shifts during the study period, 100 percent bar graphs of the most common taxa were created and F and T-tests were utilized in order to determine which of these mean taxa abundances were similar or different over the three flood stages. Percent freshwater genera abundance plots were created in order to visualize the relative amount of freshwater species that were present at the IFCB sampling station during each flood stage.

In order to analyze patterns of all phytoplankton genera abundance during the study period, a Principal Coordinates Analysis (PCO) displayed the phytoplankton genera abundance data on Euclidean axes by utilizing a matrix of inter-point dissimilarities. This analysis produced a figure that depicted similarities between samples from each flood stage. Pearson correlation vectors of the environmental data were overlaid on the figure in order to make inferences about environmental drivers of community composition.

To support these inferences, a Bio-Env + Stepwise (BEST) test using the BIOENV routine and Spearman Rank correlation methods comparing the environmental data (Temperature, Salinity, Dissolved Oxygen, Mean Daily Tide Height, Wind Speed, and Mean Daily FWIs) to the Bray Curtis similarities of the phytoplankton community data was utilized in order to statistically determine the primary drivers of phytoplankton community composition. A permutation test with 999 permutations (significance level of $p < 0.001$) ran in conjunction to verify the multivariate pattern.

In order to determine how much of the phytoplankton community composition variability these primary drivers explain, a Distance Based Linear Model (DistLM) model was run. This DistLM procedure models the relationship between multivariate data derived from a Bray Curtis resemblance matrix to environmental predictor variables. More specifically, this model was run using the "all specified" procedure and the R^2 selection criterion with 9999 permutations on the Bray-Curtis similarities of the phytoplankton community composition data compared to the square root transformed environmental data. The DistLM model was verified using a Distance-Based Redundancy Analysis (dbRDA) that is an ordination of the fitted values from a multivariate regression model.

A transition stage was present between the flooding and post-flooding stages. A second 100 percent genera abundance plot was created in order to visualize the changes in phytoplankton community composition during this stage. F and T-tests were again utilized here in order to determine significant differences between the mean taxa abundance during the flood, transition and post-flooding stages.

A second DistLM model was run in order to determine the main drivers of phytoplankton community composition between the pre-flood and post-flood stages in order to determine if the community during these stages was more influenced by the flooding event or seasonal trends. This model was also verified using a dbRDA.

3.8 Determine Size Structure Response to Flood with Time for Galveston Bay

In order to better understand the long term effects of flooding on the phytoplankton dynamics of Galveston Bay, it is important to understand the community response after the initial flooding event. In order to examine this, Abundance-Biovolume Curves (ABC) were created. ABC are a useful method in determining the degree of environmental stress in a system without the need for a control sample. This method was originally developed to assess the effects of pollution on benthic communities, although later it was found that it did not work with all benthic taxa (RaM Warwick, 1986; RM Warwick & Clarke, 1994). It has since been used to study other types of fauna (Anticamara, Zeller, & Vincent, 2010; Austen, Buchanan, Hunt, Josefson, & Kendall, 1991; Penczak & Kruk, 1999; Yemane, Field, & Leslie, 2005). The theory behind these curves utilizes knowledge about K vs r taxa (Pianka, 1970) in conjunction with information about size ranges and abundance.

This method compares each species' ranked abundance distribution to the same distribution of biomass (x-axis, log scale) with the percent dominance (y-axis, cumulative scale) (RaM Warwick, 1986). It then combines these results with knowledge that K selected species are generally present when a community is stable and approaching equilibrium and that even though smaller, r selected species may be more

numerically dominant, it is likely that these larger K selected species will still have a larger biomass than these smaller individuals combined. An example of this would be Figure 5A and would indicate an undisturbed/unpolluted system (RaM Warwick, 1986). When the opposite is true and a system becomes grossly polluted/disturbed (Figure 5C), it is likely that r selected species would have a competitive advantage and would be present in greater numbers than the larger species that would now contribute less to the overall biomass of the sample. When the system is only moderately polluted/disturbed then the distance between the lines lessens because the large species are eliminated and there is more equality in size between the biomass and numerical dominants. This is shown in Figure 5B (RaM Warwick, 1986).

The degree of community disturbance was quantified through the calculation of a W-statistic associated with these figures. The W-statistic is representative of the area between the biovolume and abundance curves (Figure 6) (RM Warwick & Clarke, 1994; Yemane et al., 2005). A positive W-statistic indicates no level of disturbance, while a negative statistic indicates some level of disturbance in the environment. More negative values indicate a greater level of disturbance and more positive values mean less disturbance in the community.

4. RESULTS

4.1 Flooding Event of 2015

The flooding event of 2015 brought enough precipitation to Texas in order to make May 2015 the wettest month on record for the state as observed by elevated riverine flows in the Trinity River. Figures 7 and 8, prepared using the USGS Romayor gauge flow data, show that peak river discharge in the Trinity River was 2.7 times higher (762 vs. 2053 m^3/sec) in 2015 than in 2014, a neutral year. These peak flows were sustained for 4.3 times longer during the flooding event in 2015. Peak FWIs lasted 7 days (5/13-5/19) in 2014, but were extended to 30 days (5/26-6/25) in 2015.

These extreme flows led to large differences in salinities compared to non-flooding years. Figures 9 and 10 are salinity maps of Galveston Bay during June of both the neutral year, 2014, and 2015, the flooding year. Darker blue areas indicate a more saline environment while the lighter blue indicates lower salinities. These figures show that there were large differences in salinity between June of 2014 and 2015 across Galveston Bay. The average salinity at six fixed stations spanning the bay was 17 in 2014, but only 3 in 2015 (data not shown).

4.2 Water Quality at the IFCB Sampling Station

Figures 11-15 illustrate the trends of the water quality and physical parameters that were examined during this study period. Water temperature showed a significant ($p < 0.05$) increasing trend from April to July (Figure 11). Salinity dropped dramatically in the middle of the study period but increased to the highest levels by the end (Figure 12). Dissolved oxygen remained constant throughout (Figure 13), while wind speed and

average daily tide height showed overall decreasing trends, although only the tide height trend was significant ($p < 0.05$) (Figures 14-15). Both were variable across time.

4.3 Determining Flood Stages

Using the cluster analysis combined freshwater discharge levels led to the creation of the three flood stages; (Figure 16) pre-flood, flood, and post-flood (Table 1) during the study period. The Pre-flood period was made obvious by the cluster analysis because they all fell into the same significant grouping. However, the flood and post-flood stage groupings were unclear. Therefore, this flooding stage was determined as the time from the end of the pre-flood period to when Trinity River discharge fell below 849 m^3/sec. After this, the post-flood stage began. This discharge rate is indicative of the discharge rate when the pre-flood stage ended and is above the peak discharge levels from the neutral year, 2014. An ANOSIM revealed that the environmental parameters differed statistically during each flood stage ($p<0.001$).

Figure 17 illustrates the large difference in mean river discharge between the neutral and flooding years, during the same calendar dates of each year, during each of the flood stages and the extreme discharge rates during the flooding event in 2015. Mean discharge was significantly ($p < 0.05$) different during the post-flood stage between years. Mean discharge was also significantly different ($p < 0.05$) during the flooding stage in 2015 compared to 2014. During the 2015 flooding stage, this parameter increased by 4.16 times (1,690 m^3/sec vs. 406 m^3/sec) compared to the pre-flood stage. Mean discharge increased by 13.41 (1,690 m^3/sec vs. 126 m^3/sec) times compared to 2014 during the flooding stage.

4.4 Phytoplankton Genera Present

During the study period, 59 phytoplankton genera and 9 functional taxa were observed (Table 2). Diatoms contributed most to the number of genera with dinoflagellates, chlorophytes and cyanobacteria making up the rest of the most diverse taxonomic groups. Functional taxa were created for cells that are commonly confused with those that look very similar, or if they had no defining features.

Table 3 shows a complete list of the genera and functional groups used in this study. Several of these genera are newly reported in the literature to Galveston Bay. These include; *Corethron, Cymatosira, Helicotheca, Licmophora, Lioloma, Meuniera, Pseudosolenia, Triceratium, Brachininium, Katodinium, Polykrikos, Scrippsiella, Spatulodinium, Spiraulax, Torodinium, Closterium, Staurastrum, Centritractus, Coccolithophore, Dictyocha, Myrionecta, Anabaena, Trichodesmium, Oltmannsiellopsis,* and *Pyramimonas.*

Some of these freshwater genera were likely seen as a result of the extreme flooding. Examples of these are; *Closterium, Staurastrum, Centritractus*, *Pediastrum, Pyramimonas, Anabaena*, *Scenedesmus*, and the elongated filamentous Cyanobacteria group, which is most likely *Oscillatoria* sp. or *Lyngbya* sp. which are both freshwater species and are commonly misidentified as one another. It is also possible that the Cyanobacteria *Merismopedia* sp. could have been introduced to Galveston Bay during the flooding as it is both a marine and freshwater species that was seen much more frequently during the flooding stage. It is likely, that due to the low taxonomic specificity of this method, the high sampling rate and that some species may be altered

during the preservation process for microscopy that this study found so many novel species.

Figure 18 is a 100 percent bar graph showing the percentage of the total phytoplankton cell densities during each flooding stage that was a member of a freshwater genera. It illustrates the introduction of freshwater species even in the southernmost portion of Galveston Bay, and that these freshwater taxa became less abundant after the flooding event.

4.5 Diversity, Abundance and Biovolume

Figure 19 illustrates the number of total individuals (N) and the total biovolume ($\mu m^{-3}/\mu L$) of each daily sample. Viewing the community as a whole in this way, in conjunction with a linear regression test, revealed a significant ($p < 0.05$) overall decreasing trend in both phytoplankton biovolume and abundance during the study period. Genera diversity, shown in figure 20 as Simpson's Diversity (1-ʎ)', significantly decreased during the flooding period ($p \leq 0.01$).

4.6 Community Composition

A one-way ANOSIM revealed that the overall phytoplankton communities differed from one another during each of the three flood stages ($p < 0.001$). More specifically, a 100 percent bar graph of the most numerically abundant phytoplankton taxa (Figure 21), revealed that within the community there was a significant decrease ($p < 0.05$) in the abundance of dinoflagellates during the flood. Entering the flooding event, there was a significant increase in the number of both diatoms and cyanobacteria, specifically the freshwater cyanobacterial genera. However, during the post-flooding

stage, the cyanobacterial abundance had decreased significantly again. Dinoflagellate and diatom mean abundance were also significantly different ($p < 0.05$) between the pre and post flooding conditions, but were similar ($p < 0.05$) between the flooding and post flooding conditions. Flagellates and *Myrionecta* sp. abundance remained similar over the flood stages.

4.7 Drivers of Variability

Figure 22 is a Principal Coordinates Analysis (PCO) that displays the phytoplankton genera abundance data onto Euclidean axes by utilizing a matrix of inter-point dissimilarities. This means that the samples that are closer together are more similar and ones that are less similar are displayed farther apart. This data shows that the community composition data separate out fairly well between the three flood stages. The first two axes explain 42% of the variation between samples.

When variability explained by a PCO is below 70 %, caution must be used when interpreting the output from this test. However, the low explained variability in this study could be a product of high variability between the samples due to the high frequency of daily sampling, that only physical parameters were studied (did not include chemical or biological factors), and the complexities associated with the growth patterns of phytoplankton.

The Pearson Correlation (> 0) vectors overlaid onto the PCO show (as a visual representation) the environmental variables that were tested as possible drivers of phytoplankton community composition variability. A BEST test revealed that mean FWI, temperature and salinity were the main drivers of phytoplankton community

composition variability. The permutation test with 999 permutations ($p < 0.001$) ran in conjunction with the BEST test showed that there was agreement in a multivariate pattern. A DistLM revealed that these three drivers cumulatively explained a total of 31% of the community composition variability, while all of the environmental parameters together explained 36%. A dbRDA analysis was run in conjunction (Figure 23). This analysis found that the model captures the multivariate pattern because the percent of fitted variation explained was above 70% (85%) and the percent of total variation explained was comparable to the PCO (31%). The dbRDA base variables are shown on the plot (correlation > 0.2). The longer the vector, the more influence that environmental parameter had on the construction of the displayed dbRDA axes.

All proportions of phytoplankton community composition variability explained by each environmental parameter were statistically significant ($p < 0.05$) except for mean daily tide height. Therefore, this environmental parameter was removed from the final DistLM because it is known that little value can be taken from P-values for individual environmental parameters after the first large P-value is encountered in sequential tests. This is because the non-significant term will affect the later results in unpredictable ways.

From what can be seen when looking at the PCO (Figure 22) and the seasonal temperature differences between April and July, it would seem reasonable that the phytoplankton community composition be primarily driven by temperature changes during the pre and post-flood periods. Using a DistLM, this was found to be the case ($p=0.001$). Temperature was found to explain 22% of the phytoplankton community

composition variability during these times. The next most influential variable was salinity, but it explained only 9% of the community composition variability ($p = 0.001$). The two tested sequentially explain 29% of the phytoplankton community composition variability ($p = 0.001$). Mean daily tide height was removed from this DistLM analysis as well because of a lack of significant proportion of phytoplankton community composition variability explained. Total percent of fitted variance from the dbRDA (Figure 24) used to verify that this model captures the multivariate pattern was 79% and the percent of total variation explained by the first two axes was 32% for the dbRDA and 43% for the PCO. This difference between the total variation explained by the PCO and dbRDA is somewhat large. This indicates that the DistLM results may not be completely verified by the dbRDA, although the overall pattern between the dbRDA model and PCO (Figure 25) seem similar.

Looking closely at the PCO of the phytoplankton community composition data from all three flood stages (Figure 22) revealed four post flood time points that were plotted within the flood time points. These points were likely a transition stage because chronologically they occur just after the end of the flooding stage (7/3-7/6). A transition stage was likely not seen between pre-flood and post-flood stages due to missed sampling dates (5/14-5/18). A one way ANOSIM revealed that the overall phytoplankton community composition was different during the transition stage compared to the post-flood stage ($p < 0.05$), but not between the transition and flooding stage.

Figure 26 shows a 100% bar graph of the most abundant phytoplankton taxa during these four stages. Mean dinoflagellate abundance was significantly ($p < 0.05$) lower during the transition stage than the post-flood stage. Mean cyanobacterial and *Myrionecta* sp. abundances were significantly ($p < 0.05$) different during the transition stage from both the flood and post-flood stages. Cyanobacteria abundance was highest during the flood stage and decreased with time. *Myrionecta* was present at its greatest abundance during the transition stage. Flagellate mean abundance remained similar between the flood and transition stage and the transition and post-flood stages.

4.8 Community Response to Environmental Stress

In order to determine how long the Galveston Bay phytoplankton community was affected by this extreme flooding event, the degree of environmental stress was calculated using ABC combined with the W-statistic. Figure 27A shows that during the pre-flood period, the phytoplankton community was dominated by fewer, yet larger species. Indicating an undisturbed system. In contrast, during the flood (Figure 27B) the community was dominated by greater numbers of smaller species, indicating gross disturbance. By the post-flood stage (Figure 27C), the lines lie on top of one another indicating greater equality in size between the biomass and numerical dominants. This is known to be an indication of moderate disturbance and reveals that the community was headed back to being undisturbed, which occurred by August 14, 2015 (Figure 27D). This means that there were a total of 67 days until the community returned from being dominated by smaller species (disturbed) to being dominated by fewer, larger genera (undisturbed) from the first day of the flooding. It took 44 days since the final day of the

flood to return to the community size structure seen during the pre-flood stage. Although this analysis reveals a change in the size structure of phytoplankton, additional analysis of this time series needs to be conducted in order to determine if the phytoplankton community composition returns to the pre-flood conditions.

5. DISCUSSION

5.1 Physical Disturbances in Galveston Bay

5.1.1 Rivers/Freshwater Inflows

Rivers are important to estuarine phytoplankton diversity because they bring in terrestrial nutrients and increase energy in estuarine environments. FWIs have the potential to either flush out phytoplankton or start blooms (De Madariaga, González-Azpiri, Villate, & Orive, 1992; H. W. Paerl, 2009). High FWIs support nanoplankton (< 20 µm) because they grow quickly. They also support large, heavy taxa because they can be suspended in shallow and turbulent water (Costa, Huszar, & Ovalle, 2009). Lower river flow can lead to the presence of many large, slow growing organisms in estuarine systems including dinoflagellates (Costa et al., 2009).

The relationship between Galveston Bay phytoplankton and FWIs has been well studied under neutral conditions and using less fine scale methods as the IFCB (Dorado et al., 2015; Örnólfsdóttir et al., 2004a; Örnólfsdóttir, Lumsden, & Pinckney, 2004b; Quigg, 2011; D. L. Roelke et al., 2013). In Galveston Bay, diatoms can be found with a range of inflows, while dinoflagellates are generally associated with low FWIs (Dorado et al., 2015). This is consistent with other estuarine systems (Chan & Hamilton, 2001). Like other estuaries, Galveston Bay phytoplankton community composition shifts due to inflow (Dorado et al., 2015; Mitrovic, Hardwick, & Dorani, 2011; D. L. Roelke & Pierce, 2011; Spatharis, Tsirtsis, Danielidis, Do Chi, & Mouillot, 2007). These shifts usually occur in May or right before because this is when the FWIs are highest into Galveston Bay (Longley, 1994; J. Pinckney, 2006; Quigg, 2011).

During more typical years there are distinct North to South salinity and FWI influence gradients in Galveston Bay with waters being less saline near the river mouths and more saline near the Gulf of Mexico. This North to South gradient has effects on phytoplankton diversity as well as biomass. The taxa present have been shown to be dependent on nutrition sources, growth rates and entry from rivers (D. L. Roelke et al., 2013). Pulsed fluvial inputs into Galveston Bay from the Trinity River are known to prevent blooms near the river mouth and result in less phytoplankton biomass because of the high energy that these inputs create in addition to a simultaneous increase in secondary productivity (Buyukates & Roelke, 2005; Jeong et al., 2005; D. Roelke, 2000; D. Roelke, Eldridge, & Cifuentes, 1999).

Diatoms have the highest biomass and greater diversity in these localized areas (Dorado et al., 2015). Near the San Jacinto River, where the flows allow for growth, cyanobacteria, haptophytes and euglenophytes do not respond to FWIs as much as diatoms (D. L. Roelke et al., 2013). This may be due to differences in feeding habits (mixotrophy diazotrophy), the nutrient storage capacity of diatoms, and being more affected by hydraulic displacement. In contrast, diatom growth rates exceed the normal flushing rate in Galveston Bay (Dorado et al., 2015). The phytoplankton communities in the middle portion of Galveston Bay have been shown to be affected both by hydraulic displacement and changes with nutrient additions (Dorado et al., 2015).

In the Southern portion of this bay, under low stress conditions, dinoflagellates and cyanobacteria are known to be more abundant than in the Northern portions (motility is a good quality with low tides) (Dorado et al., 2015). With higher FWIs the

dinoflagellate abundance decreases, while diatom abundance increases when the inflows come from San Jacinto River (D. L. Roelke et al., 2013). Conversely, the green phytoplankton lineages, cyanobacteria, and haptophytes are reduced with increasing inflows from Trinity River but increase with inflows from the San Jacinto River (D. L. Roelke et al., 2013).

These conditions under more neutral years provide a baseline that can be used to compare to the changes that were seen during this extreme flood event. The changes to the phytoplankton community during the 2015 flooding event were similar to what was seen during this study period, with some important changes. At the sampling station, in the Southern portion of Galveston Bay during the pre-flood conditions, dinoflagellates were the dominant taxa, as expected. During the flood, when FWI were greatly increased and salinities abruptly decreased compared to a neutral year, the dinoflagellate abundance decreased and diatom abundance increased.

Although the overall results of the changes were similar to the neutral years, it is important to know that this entrance of freshwater genera takes place with extreme events, even at the southernmost portions of Galveston Bay. Flooding caused by hurricanes has been shown to have a similar effect on the phytoplankton in marine systems. In a study of a tropical lagoon, freshwater cyanophytes were shifted from occurring only near the rivers to the middle of the lagoon as well (Srichandan et al., 2015). During this hurricane it was found that phytoplankton taxa have the ability to respond to different salinity regimes (Srichandan et al., 2015). During riverine flooding, Chan and Hamilton (2001) found that chlorophytes were introduced into the system.

Freshwater cyanobacteria increased with flows from the Trinity River, instead of only the San Jacinto River, during this study due to the entrance of freshwater genera. This is likely due to the extreme quantity of freshwater that entered into the bay allowing for these genera to be flushed down even to near the mouth of the bay. Cyanobacteria have a special advantage during this study period because they tend to already be selected for in warmer months (Dorado et al., 2015; Örnólfsdóttir et al., 2004b); however these past studies utilized High Performance Liquid Chromatography and may have been detecting the cyanobacterial community that is too small for the IFCB to image. In the future, studies should be performed looking at the both the phytoplankton within the sampling range of the IFCB and the picophytoplankton (0.2 -2 μm). It is likely that including them in a study such as this could give a much better understanding of the phytoplankton community composition as a whole. This is made especially important because, some estuarine systems, these picophytoplankton can make up ~35-44% of the total chlorophyll biomass (Gaulke, Wetz, & Paerl, 2010). In Pensacola Bay, Florida cells < 5 μm average over 70% if the total phytoplankton biomass (Murrell & Lores, 2004).

It is important to emphasize that since our sampling station is located in southern Galveston Bay, farthest from the rivers, and because it has been shown in many systems that FWIs have diminished effects farther away from rivers (Chan & Hamilton, 2001; Choudhury & Pal, 2011; Dorado et al., 2015; Hall, Paerl, Peierls, Whipple, & Rossignol, 2013; H. W. Paerl et al., 2003; D. L. Roelke et al., 2013; Russell, Montagna, & Kalke, 2006), it is likely that these flooding effects had an even larger impact on the

communities nearer to the rivers and that the relative cyanobacterial abundances were likely higher in these more Northern areas.

These freshwater cyanobacteria have the potential to cause blooms and may not have the potential to support the higher trophic levels that generally dwell in this area. The entry of freshwater cyanobacteria also indicates that the level of flooding could have been so extreme as to cause a complete turnover of the water in the bay, from being more marine to more fresh. Many of the larval/adult fish and benthic organisms may not have been able to survive in these conditions and therefore might have been forced to flee or were flushed from the system as well.

5.1.2 Extreme Flooding

Changes to phytoplankton community abundance and composition during the extreme flooding event of 2015 are likely ultimately linked to hydraulic flushing within the system. Extreme FWIs into Galveston Bay lowered the residence time of the water and increased energy within the bay. This caused hydraulic flushing of the non-motile plankton that could not reproduce faster than they were being washed out. This led to the overall decrease in phytoplankton biovolume and abundance in spite of the increasing temperatures over the study period which is normally positively correlated to phytoplankton concentrations in Galveston Bay (Dorado et al., 2015). This coupled with the effects of hydraulic flushing and the resulting salinity decrease are likely why FWI and salinity were the main drivers of phytoplankton community composition shifts during this study. Temperature was another major driver, that was important overall in shaping the phytoplankton community composition, although because of the relatively

large effect it had mostly during the pre and post-flooding stages, this environmental variable was most likely not as important of a driver during the flooding stage.

These three environmental drivers of phytoplankton community composition explained 31% of the total community composition variability. The remaining significant drivers explained 36%. These levels of explained community composition variability were lower than what was expected given the intensity of the FWIs. However, because this level of sampling frequency has never before been conducted in Galveston Bay, therefore it is difficult to determine how much variability is introduced by this high level of sampling alone.

These effects of hydraulic flushing on phytoplankton biomass is seen during neutral years near the Trinity River (D. L. Roelke et al., 2013) and in other estuarine systems (Balch, Drapeau, Bowler, & Huntington, 2012; García, Juanes, Álvarez, Revilla, & Medina, 2010). In an estuary in Florida, extreme flooding in July led to substantially lower biomass even though the nitrate concentrations increased fivefold (Mortazavi, Iverson, Landing, Lewis, & Huang, 2000). However, by October, phytoplankton biomass levels had returned to pre-flood levels.

Reduced biomass could indicate that increased flooding disturbance events in Galveston Bay could lead to overall less nutrition and possibly lower abundance of higher trophic levels. Extended periods of freshwater floods have the potential to cause oyster kills in the Mississippi sound (Butler, 1952; Hildebrand & Gunter, 1953) and Texas estuarine productivity is often lower during flooding after prolonged droughts (H. Odum & Hoskin, 1958; H. T. Odum & Wilson, 1962).

Hydraulic flushing coupled with the harsh conditions of the high energy waters likely caused the shift from the slower growing dinoflagellates to faster growing and non-chain forming species and the entrance of freshwater genera into the bay. We can infer from past studies that these faster growing species would likely be diatoms and cyanobacteria, which is consistent with the results of this study (Dorado et al., 2015; Örnólfsdóttir et al., 2004b).

In this study, diatoms were the most abundant taxa and significantly increased during the flooding event. This could be because, in addition to their relatively high growth rates, when suspended in highly turbulent water, nutrient uptake can increase by greater than 50% in cells larger than 60 µm (Karp-Boss, Boss, & Jumars, 1996). This could be compounded by knowing that diatom relative abundance is positively correlated to nitrogen and phosphorous concentrations (Schiebel et al., 2004) and correlated negatively to water column stability (Li, 2002).

However, although diatoms were the most abundant taxa on average, the ABC revealed that there was indeed a size shift that led to dominance by smaller cells during the flooding event. This is likely because smaller diatoms became more prevalent, such as single cells of *Thalassiosira* and small pennate diatoms, compared to during the pre-flood stage when more chain forming diatoms such as *Chaetoceros* and rodlike diatoms were more prevalent.

This ABC model was originally created using the basis of r vs. K selection of species. Margalef (1978) historically describes diatoms as r selected and dinoflagellates as K selected taxa. He also describes that diatoms are able to better survive in more

turbulent conditions than dinoflagellates. However, more recently, it has been suggested that phytoplankton functional groups are more complex than r vs K strategists alone (Smayda & Reynolds, 2001, Reynolds et al, 2002). In spite of this, the ABC model is still useful for determining disturbance in the Galveston Bay phytoplankton community because, during the flooding, chains were broken, resulting in smaller cells and only faster growing taxa were allowed to prevail due to the lowered residence times. Therefore, the cells that could survive in these conditions, including the phytoplankton that were able to survive and reproduce as they were likely being flushed through the estuary, acted as r selected taxa due to these constraints. According to Smayda & Reynolds, 2001, these phytoplankton are likely a part of the R (ruderal) types that occur in physically disturbed water. These do well in flooding conditions because they are shear resistant, are efficient light harvesters and have higher growth rates than most dinoflagellates. Based on this reasoning, the diatoms present during the flooding are likely the spring bloom species (Smayda & Reynolds, 2001).

However, the results of the ABC may have partially been seen due to a caveat of IFCB sampling, where chains are counted as individual cells. This means that during the pre-flood stage, when there was less energy in the system and the phytoplankton were more likely to form chains, that the abundance of genera such as *Thalassiosira* could have been underestimated compared to the flood stage when these chains were likely to be broken. Therefore, these cells would likely have been counted individually instead of as a single chain. This is a known caveat of IFCB sampling and may reduce the validity of the ABC used in this study.

These shifts in community composition overall corresponded with a decrease in diversity during this extreme flooding event. This decrease coupled with the lack of blooms indicates low resource use efficiency by the phytoplankton. These results are comparable to other systems where flooding periods have decreased diversity and been shown to be an indicator of more stress factors for phytoplankton, less stable communities and lower resource use efficiency (Nagy, Bidegain, Caffera, Blixen, & Ferrari, 2006). This is emphasized by research that showed a positive correlation between diversity and resource use efficiency and this relationship was strongest in times of low diversity (Ptacnik et al., 2008).

5.1.3 Wind Driven Mixing and Tides

Wind mixing in shallow estuaries increases the energy in the system; it can change mortality rates of phytoplankton due to physical damage and reduce stratification (Berdalet, 1992; H. W. Paerl, 1988; Pollingher & Zemel, 1981; Thomas & Gibson, 1990). These changes can lead to higher diversity as has been seen in the in Pearl River Estuary, near the South China Sea, where the diversity of phytoplankton is higher in the rainy season, but the cell abundance is greater in the dry season (Huang et al., 2004). Wind mixing can also increase biomass and cause diatom blooms in low nutrient estuaries when mixing brings up benthic nutrients (Bowman, Esaias, & Schnitzer, 1981; Iverson, Curl, O'Connors, Kirk, & Zakar, 1974). Nutrient uptake can also be increased by more than 50% in cells where the water is flowing against the cell wall, due to water making the diffusive boundary layer thinner in cells that are larger than 10 µm (Karp-Boss et al., 1996). However, mixing can also lead to lower primary productivity and

chlorophyll-*a*, because the phytoplankton spend less time in the photic zone (Demers, Lafleur, Legendre, & Trump, 1979; Demers & Legendre, 1981; D. L. Roelke et al., 2013). This may be unimportant for Galveston Bay because the phytoplankton are not limited by light due to its shallow nature (~2-3m in most of the Bay) and constant wind driven mixing (Dorado et al., 2015). It has been suggested that winds in Galveston Bay can lead to a stable and diverse community (random distribution of cells) and maintenance of nanophytoplankton dominance (sediment resuspension/nutrient introduction) (Örnólfsdóttir et al., 2004b).

Physical and community variability in the estuarine environment can also be driven in part by tides (Findlay, Pace, & Fischer, 1996). Tides cause mixing, and the resuspension of benthic nutrients and phytoplankton (J. Cloern, Cole, & Edwards, 1996). They also transport water horizontally into coastal systems that can lead to phytoplankton patches (Franks & Chen, 1996). In more open systems such as in Southern Florida, tides have the potential to increase phytoplankton biomass and alter community composition in the shallow systems just offshore due to sediment resuspension (Phlips & Badylak, 1996). Microtidal estuaries, such as Galveston Bay, have maximum turbidity during flooding of rivers because they do not have tidal sedimentary resuspension (Monbet, 1992). They generally have lower suspended sediment loads than macrotidal estuaries (Nichols & Biggs, 1985). Tides are also important in the recruitment of higher trophic levels. High ichthyoplankton abundance has been associated with low tides due to advection, high prey abundance, aggregation

response, and larval supply. This can influence spatial recruitment patterns of fish species (Kingsford & Suthers, 1996).

Winds and tides have the potential to alter phytoplankton community composition in Galveston Bay. However, during this study, wind speed explained a significant but small (5%) of the total phytoplankton community composition variability while mean daily tide height explained none of the variability ($p > 0.05$). This may be in part due to the intensity of the flooding event masking the effects of these variables. Seasonal patterns of wind and tides could also have a larger effect on phytoplankton community composition in Galveston Bay near the Gulf of Mexico, however more studies should be conducted. In addition, the differences in time scales between changes in tide and wind events compared to the daily sampling frequency of this study could have an impact on how much variability is explained by these physical parameters.

For example, although mean daily tide height gives us an idea of the total tide height range during each day, in the future it would be beneficial if a study could be done with a higher frequency of sampling in order to determine the individual effects of the flood and ebb tides on the phytoplankton at the IFCB station. This is important because, in a salt marsh estuary, it was found that when water with low phytoplankton biomass entered into the system via a flood tide, along with the effects of grazing and settling, this caused large decreases in biomass (47-51%) and changed the community composition (Wetz, Hayes, Lewitus, Wolny, & White, 2006). Although it is likely that the effects of tide in Galveston Bay will not be as intense because the mean tidal range is 11.3 times higher (1.7 m) in this estuary than in Galveston Bay. In addition, other studies

have shown that tides can lead to changes in grazing pressure that can also affect phytoplankton community composition near the mouth of estuaries (Lewitus, Koepfler, & Morris, 1998; Lucas & Cloern, 2002; Lucas, Koseff, Monismith, Cloern, & Thompson, 1999; Morris, 2000).

In addition, it may also be beneficial to study the effects of wind on phytoplankton community composition at shorter time scales. A study of phytoplankton in Mediterranean coastal waters that took in situ flow cytometer samples every 30 minutes, found that phytoplankton variations occurred over several days after wind events (Thyssen, Mathieu, Garcia, & Denis, 2008). An additional study, performing high frequency sampling, found that winds can change the phytoplankton community composition due to mixing and resuspension (Pannard, Bormans, & Lagadeuc, 2007). However, some of these patterns seem to be due more to the circulation patterns that winds have on the system, rather than the shear stress associated with winds on the phytoplankton cells themselves. Studies that have sampled on the scale of hour(s) to every few days have found that chlorophyll-*a* variability can be driven by wind when they cause changes in water circulation patterns (Abreu, Bergesch, Proença, Garcia, & Odebrecht, 2010; Litaker, Duke, Kenney, & Ramus, 1993).

5.2 Post-Flood Transition Stage

During the transition stage between the flood and post-flood stages, there was a steady decrease in cyanobacteria abundance. This is consistent with decreasing levels of freshwater inflows that would restrict the entry of these genera into the system. During the post-flood stage, dinoflagellates increased and were at their highest abundance since

the flood stage. However, dinoflagellates did not show a steady increase over these periods as there was a higher mean dinoflagellate abundance during the flooding stage than the transition stage.

Myrionecta sp. showed a pattern of increased abundance during the transition stage. Members of this genus typically ingest the flagellate cryptophyta and retain their plastids for use in autotrophy within the protist (Yih, Kim, Jeong, Myung, & Kim, 2004). These protists may be occurring in response to the flagellate taxa in this study and could be controlling their abundance. A single *Myrionecta rubra* has the ability to ingest 8.9 cryptophytes per day, which gives them the ability to exert considerable pressure on their prey (Yih et al., 2004). During the transition stage, mean flagellate abundance was lowest than during any other stage, although there were no significant changes to the flagellate mean abundance during the entirety of the study period. However, it is difficult to determine the effects on this taxon alone when they are included in the same group as other flagellates as they are in this study.

Cryptophytes would likely be selected for during a flooding event, because they survive in either freshwater or marine ecosystems and have a maximum growth rate that is comparable to diatoms (Gervais, 1997). However, *Myrionecta* sp. prefer cryptophytes with an equivalent spherical diameter of ~5.3 µm (Yih et al., 2004). Cells of this size would not be easily identifiable using an IFCB and may have been overlooked in this study. However, a Staining IFCB (IFCB-S) has recently been developed that will allow for IFCBs to live cell fluorescent stain protists that do not contain chlorophyll (Boyer, Christian, & Stanley, 1993). This will allow for a closer look at protists that have been

previously overlooked, and will provide fine scale insight into the predator/prey relationships between them and phytoplankton.

5.3 Changes with Climate

The three major hazards to estuaries are human activity, global climate change and extreme events (Jennerjahn & Mitchell, 2013). Galveston Bay is vulnerable to all of these. There have been many studies within this bay looking at the effects of human activities, such as the addition of anthropogenic nutrients (Dorado et al., 2015; Örnólfsdóttir et al., 2004a, 2004b; D. L. Roelke et al., 2013), and invasive species into the bay (Steichen, Denby, Windham, Brinkmeyer, & Quigg, 2015; Steichen, Windham, Brinkmeyer, & Quigg, 2012), so here I will focus on global climate change and extreme events. In addition, it is important to study climate oscillations in regards to phytoplankton in estuarine systems, because sometimes these oscillations can overpower the effects of anthropogenic nutrient inputs (H. W. Paerl, Rossignol, Hall, Peierls, & Wetz, 2010).

Floods are the most common natural disaster in the United States. They are produced by either riverine inputs or hurricanes. This is made especially important because, due to climate change, it is expected that there will be both an increase in river flow in the Southern United States (Groisman et al., 2004) and an increase in the frequency and intensity of storms in Galveston Bay and the Western Atlantic (Figure 28) (Bender et al., 2010; Emanuel, 2005; Goldenberg et al., 2001; Hartmann et al., 2013; Levinson, Vickery, & Resio, 2010; Warner & Tissot, 2012; Webster, Holland, Curry, & Chang, 2005).

5.4 El Niño

During El Niño periods, in areas where precipitation is increased and riverine flooding events are more common, similar overall results have also been found. Sathicq et al. (2015) saw significant decrease in phytoplankton diversity during El Niño periods. In addition, they too saw a reduction in phytoplankton biomass and density and a change in species proportion. In the Rio de la Plata estuary, El Niño years were characterized by diatom dominance compared to La Niña and neutral years. Cyanobacteria also competed well during El Niño years in this system because they are better adapted to high flow rates and increased turbulence (Sathicq, Bauer, & Gómez, 2015).

An earlier study found that the 1982-83 El Niño caused drop in phytoplankton abundance and diversity in 1984. This community began recuperating in 1985 and recovered in 1986, and that these increases were larger than previously seen (Garate-Lizarraga & Beltrones, 1998).

El Niño has also been shown to have effects on fish diversity, abundance and community composition. One study in the Patos Lagoon, in Brazil, found that the high rainfall associated with El Niño caused fish abundance to be 5 times lower. This study also found an introduction of freshwater fish species into the estuary. It took 18 months for the fish assemblage to resemble pre-El Niño conditions. This turnaround was thought to be a product of high productivity, due to nutrients being released from the sediments (Garcia, Vieira, & Winemiller, 2001, 2003). Both of these examples show that it took over a year for phytoplankton and fish communities to recover to pre-El Niño conditions. This indicates that, during this study, although the ABC showed that the

phytoplankton community returned back to being undisturbed, it was likely not recovered to the pre-flood assemblage.

5.5 Hurricanes

The second type of estuarine flooding, from hurricanes, is associated with floodwaters that alter salinity gradients which can produce similar results to the flooding event seen in this study of Galveston Bay (H. W. Paerl et al., 2001; Peierls, Hall, & Paerl, 2012; Srichandan et al., 2015). Severe hurricanes have also been known to alter phytoplankton community composition, much like floods. Differences in landfall location, wind speed, the path taken after landfall, rainfall rate, surface runoff and speed of passage can all influence whether a hurricane can either trigger an algal bloom or cause an increase in hydraulic flushing and turbidity that discourages bloom formation (Kumar, Mishra, Equeenuddin, Cho, & Rastogi, 2016). More specifically, if a tropical storm moves through an estuary's watershed, it is more likely that nutrients and organic matter will be introduced into the system compared to when a tropical storm moves over or along the edges of the estuary (Mallin & Corbett, 2006; Mallin et al., 2002). Many studies have shown similar results to those in this study following tropical storms by finding decreases in phytoplankton productivity (Mallin et al., 2002; H. W. Paerl, Pinckney, Fear, & Peierls, 1998).

In the Neuse River Estuary, in North Carolina, different hurricanes/tropical storms and the conditions just before determined the effects of the event on phytoplankton biomass (Wetz & Paerl, 2008a). For example, a tropical storm that resulted in higher phytoplankton biomass mixed previously stratified waters (suspending

benthic nutrients) when the phytoplankton were already Nitrogen limited. A smaller, tropical depression led to localized blooms and mixed the water column. In contrast, Hurricane Isabel arrived when the system was already well mixed and when nutrient concentrations were high. This led to less favorable growth conditions for phytoplankton less than one month after the storm (Wetz & Paerl, 2008a) partially due to a 2 fold increase in ciliate biomass (Wetz & Paerl, 2008b). This could be the case with Galveston Bay, because of the increase we saw in *Myrionecta* during the post flood transition stage. In the future, studies should be done looking at grazing pressures associated with extreme inflow events.

After flushing events, when the discharge lessens and residence time begins to increase, nutrients from up the watershed could be retained by the estuary and promote cyanobacterial blooms (H. W. Paerl & Huisman, 2009). Blooms like these have been observed after flooding events where FWIs were intense enough to flush out phytoplankton biomass in the Northern part of the Neuse River Estuary (Boyer et al., 1993). The dinoflagellate *Heterocapsa* sp. bloomed that winter. This was thought to have been influenced by the flooding event earlier in the year (Boyer et al., 1993). Blooms that are the result of these hurricanes, can lead to hypoxia/anoxia and cause fish kills that can also harm the benthic community (Mallin et al., 2002; Mallin et al., 1999). There have been many instances when blooms can occur weeks to months after cyclones or flooding when the hydraulic flushing lessens and light again becomes available (Murrell, Hagy, Lores, & Greene, 2007; H. W. Paerl et al., 2001; Peierls, Christian, & Paerl, 2003)

Blooms such as these are even more likely to occur if there is a period of drought soon after flooding (H. Paerl & Fulton III, 2006; Uwins, Teasdale, & Stratton, 2007). Galveston Bay is at risk of experiencing lower FWIs because of population growth (19.2 million by 2050) within the watershed (Johns, Hess, Kaderka, McCormick, & McMahon, 2004). Just after drought periods, with the return of FWIs to Galveston Bay, the community has been dominated by dinoflagellates, these phytoplankton have the potential to have produced cysts during the drought that can bloom with the return of FWIs (personal correspondence). In spite of this, large FWI events that have the ability to flush out plankton, which can be expected to increase with climate change, could have the potential to improve water quality and reduce harmful algal blooms under the right conditions (Mitrovic et al., 2011; D. L. Roelke et al., 2013). The extreme flooding event of this study likely had this effect.

6. CONCLUSIONS

Changes in weather over different time scales can lead to alterations in phytoplankton community structure (J. E. Cloern & Jassby, 2010). Variation in climate, such as during El Niño years, can cause shifts in the normal annual cycles of phytoplankton (Di Lorenzo et al., 2008). Global climate change is likely the cause of the decrease in global net primary productivity since 1999 due to greater stratification (decreases nutrient exchange) in the low-latitude oceans (Behrenfeld et al., 2006; Finkel et al., 2009). In addition to changes in overall primary productivity, there is likely to be global community composition shifts due to the northward movement of diatoms that prefer cooler waters (Marinov et al., 2013). Dinoflagellates also may become more prevalent in temperate areas as these areas become warmer and more stratified (Barton, Irwin, Finkel, & Stock, 2016). Knowing how changes in physical parameters of the ocean affect phytoplankton community structure can provide a better understanding of how the communities might be altered by climate change.

With climate change, by 2100 in Galveston Bay, exceedance probabilities of flooding could double for the impact of large hurricanes (Ike) and increase 6-7 times for smaller surges that come with less intense hurricanes (Rita). Using a conservative scenario that is a linear continuation of the past century, these inundations from smaller storms will shift from occuring once every 6.6 years to once annually, but for the IPCC A1F1 scenario, this level of inundations could be occuring by 2050 (Warner & Tissot, 2012). In addition, climate change is expected to double the frequency of El Niño events

from 1 every 20 years to 1 every 10 (Cai et al., 2014). Therefore, it is important to understand the effects of these extreme events that have the potential to cause flooding along the Galveston Bay watershed. Knowing the effects this will have on the phytoplankton will allow for a foundation in which to understand the effects they could have on Galveston Bay as a whole as their frequencies increase.

Extreme FWI events in Galveston Bay lead to a higher flushing rate, lower residence time and higher energy within the system. This is likely what led to a shift from slower growing and chain forming genera to faster growing and non-chain forming genera and a decrease in diversity, biovolume and abundance. Large quantities of freshwater entering into the estuary also led to the introduction of freshwater phytoplankton. An increase in extreme flooding frequencies due to climate change has the potential to negatively impact higher trophic levels in this system and promote blooms when flooding events are followed by drought.

Although many studies on phytoplankton community composition and ecology have been conducted in Galveston Bay using microscopy and High Performance Liquid Chromatography (Dorado et al., 2015; Örnólfsdóttir et al., 2004a, 2004b; H. W. Paerl et al., 2003; J. L. Pinckney & Lee, 2008; D. L. Roelke et al., 2013), daily sampling, coupled with IFCB analysis, has allowed for a finer-scale assessment of the phytoplankton community composition variability and its relationship to extreme changes in the environment. This is important because the fast growth rates of phytoplankton mean that they quickly respond to a large range of changes in the environment. This, coupled with the likelihood that by the next century flooding events

could occur on an annual scale in Galveston Bay, makes it extremely important to understand the effects of these events at the base of the food web.

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APPENDIX A: FIGURES

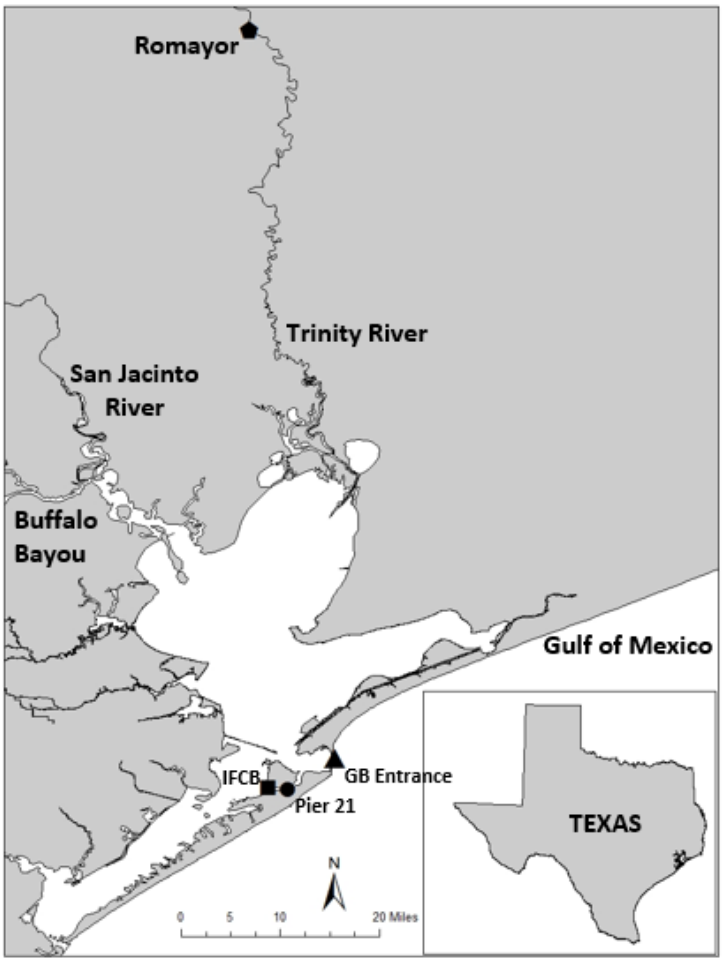

Figure 1 Galveston Bay, Texas: Sampling locations for this study. IFCB Sampling Station, NOAA Pier 21 (wind speed), NOAA Galveston Bay Entrance Station (Tide Height), and USGS Romayor (FWI)

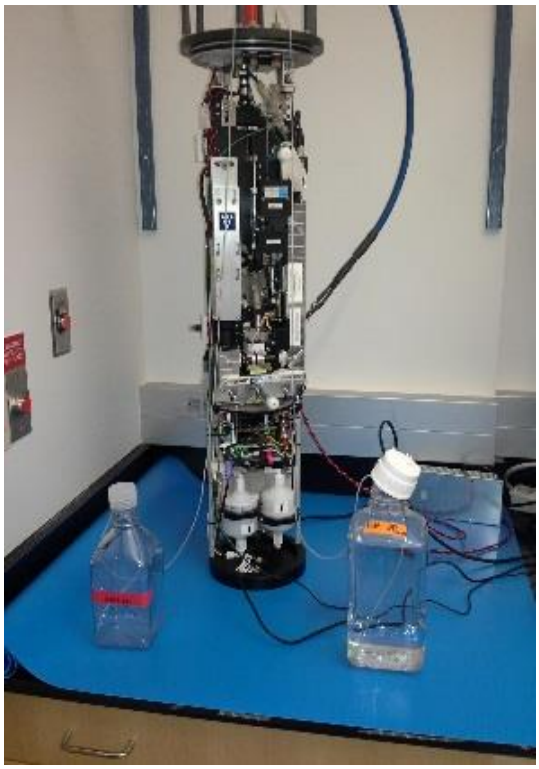

Figure 2 Imaging FlowCytobot in benchtop mode

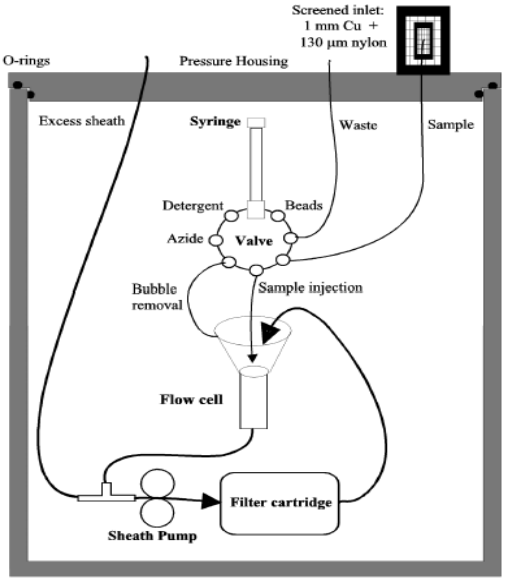

Figure 3 Schematic of IFCB fluidics system. Taken from Olson & Sosik, 2007.

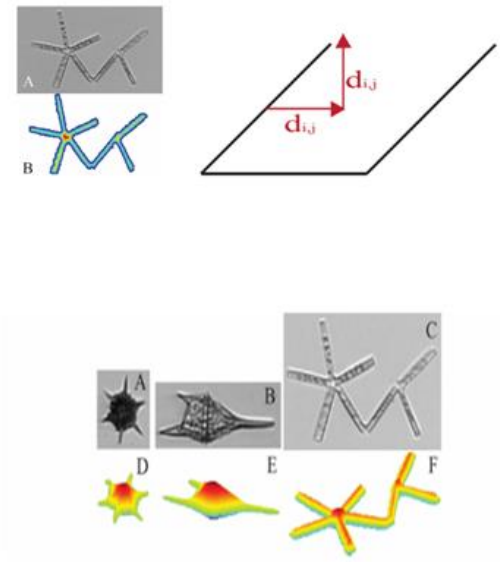

Figure 4 A visual description of biovolume calculations as described in Moberg & Sosik, 2012. This method was utilized to calculate cell biovolumes for IFCB samples.

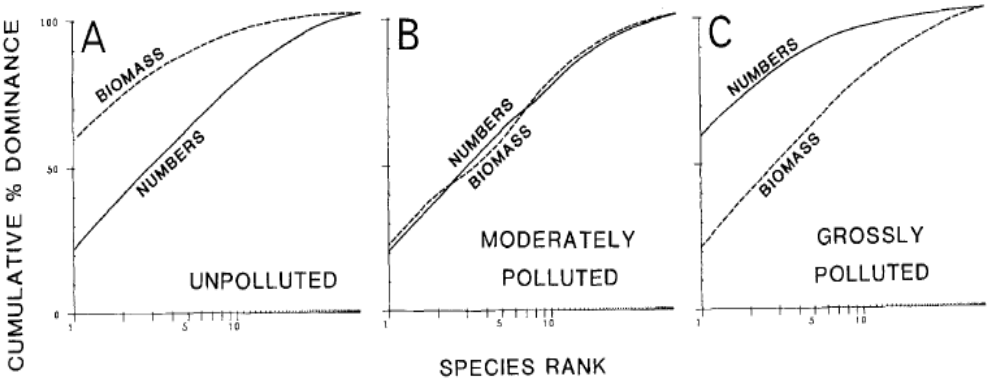

Figure 5 Taken from Warwick (1986) showing the three stages of pollution/disturbance associated with ABC curves

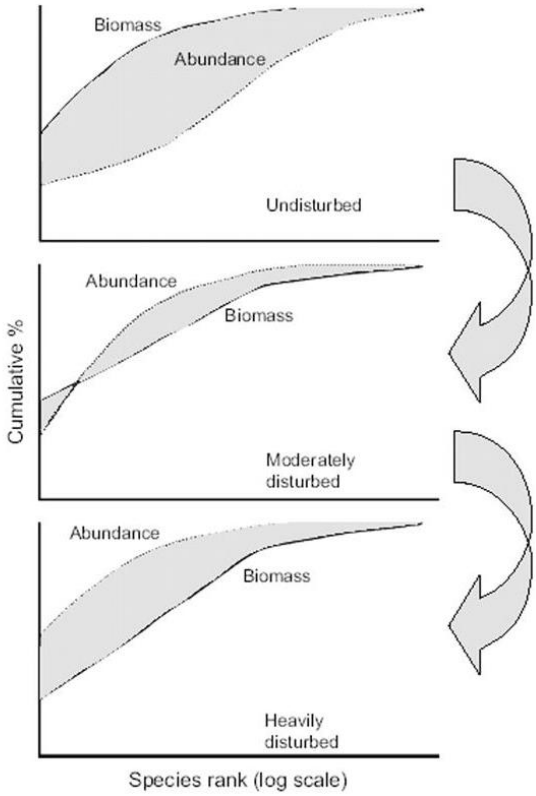

Figure 6 An additional sample showing ABC curves utilized to show disturbance. The area in gray is used to calculate the W-Statistic. Figure taken from Yemane et al., 2005.

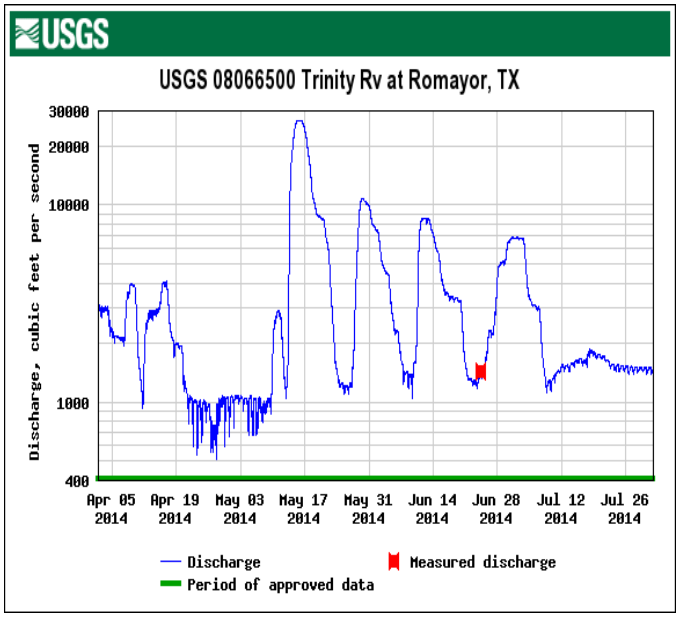

Figure 7 Freshwater discharge from the Trinity River from April-July 2014. Taken from USGS Romayor station.

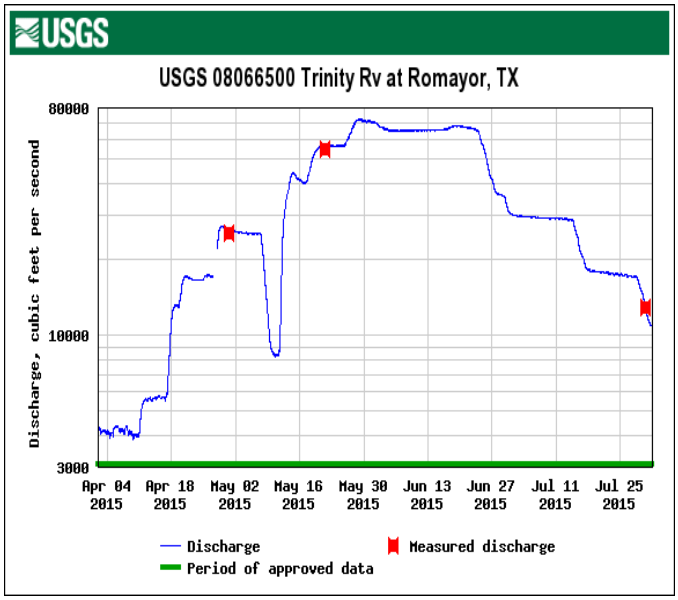

Figure 8 Freshwater discharge from the Trinity River from April-July 2015. Taken USGS Romayor station.

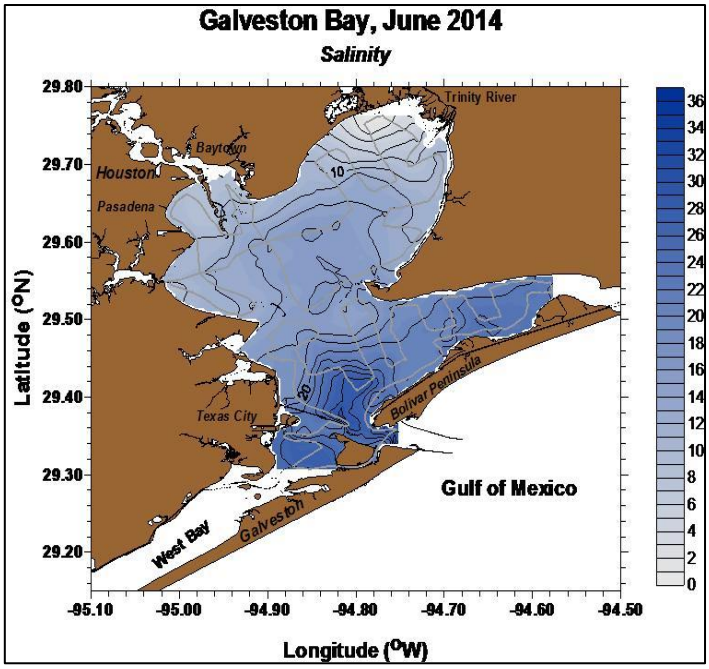

Figure 9 June 2014 salinity map of Galveston Bay, interpolated from Galveston Bay Project data

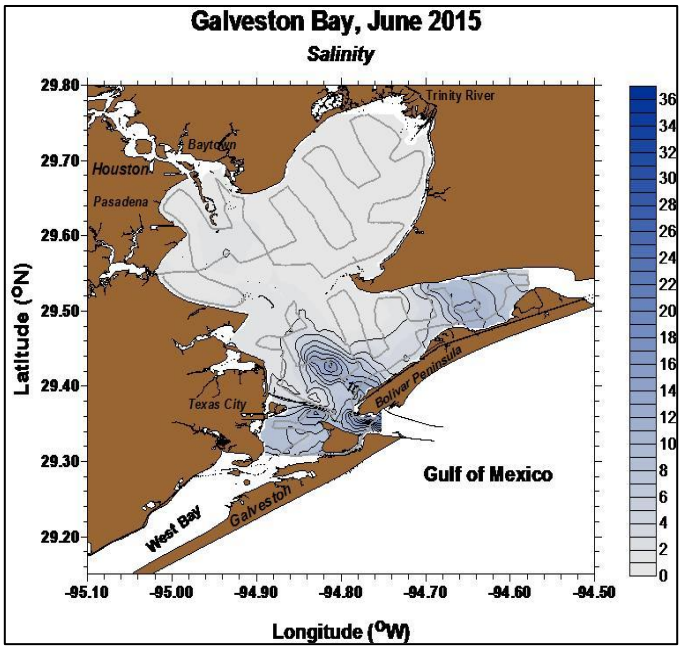

Figure 10 June 2015 salinity map of Galveston Bay, interpolated from Galveston Bay Project data

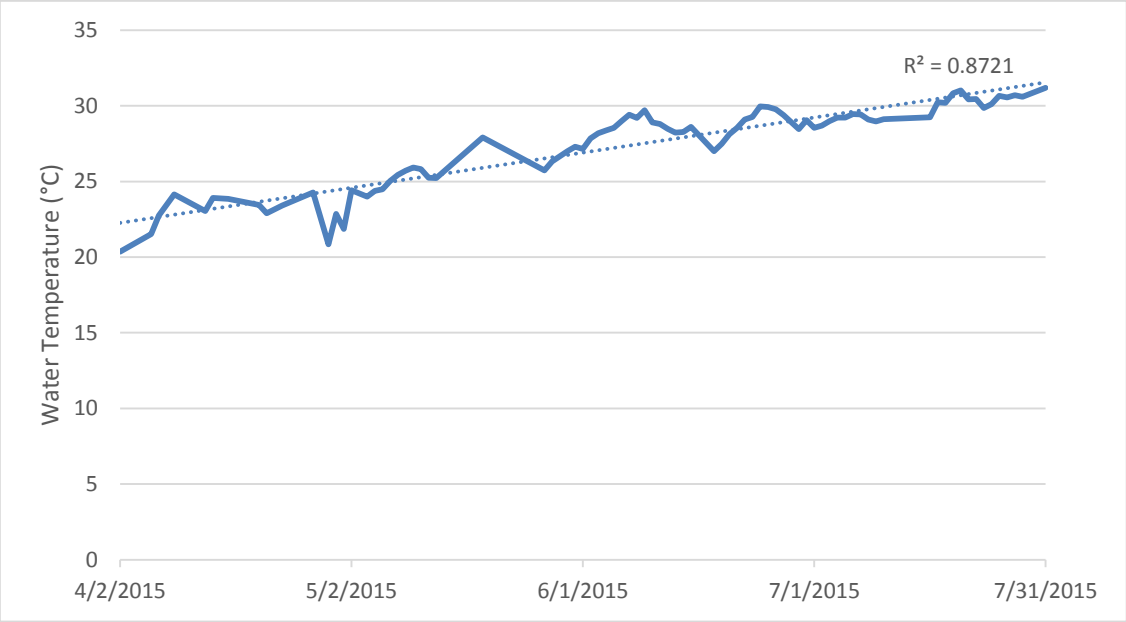

Figure 11 Water temperature at IFCB station.

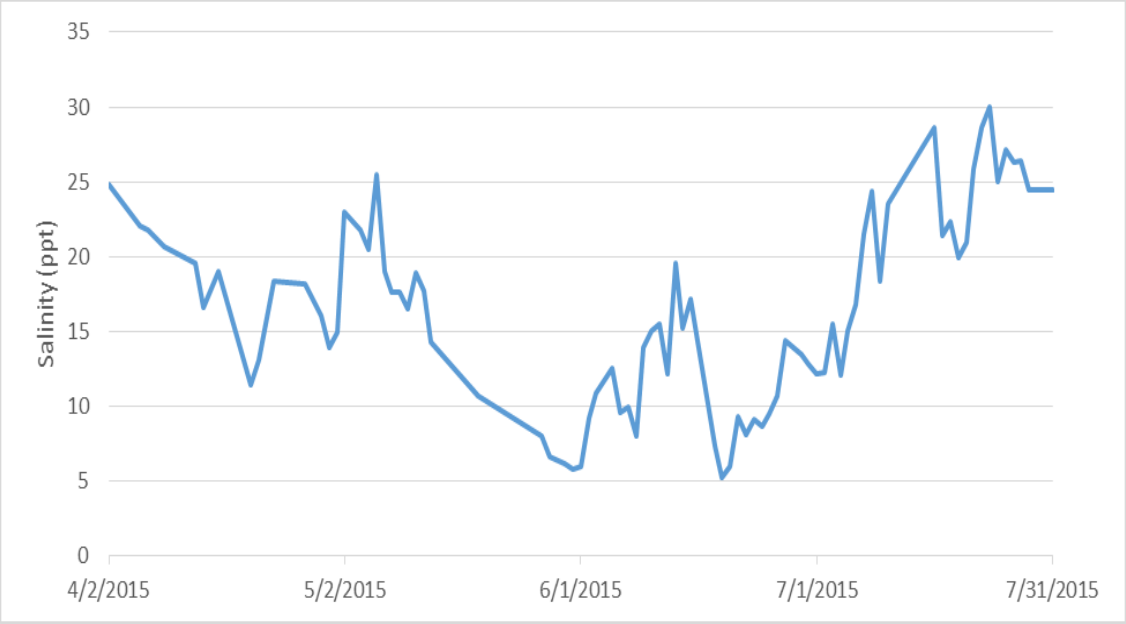

Figure 12 Surface salinity at IFCB station.

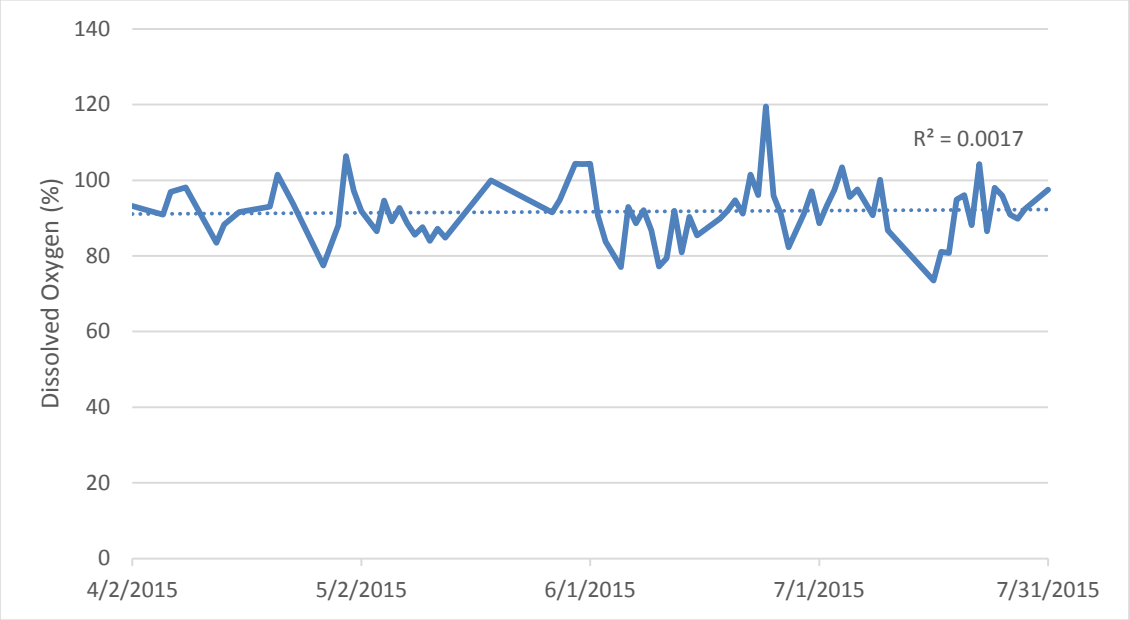

Figure 13 Dissolved Oxygen (%) of sample at IFCB station.

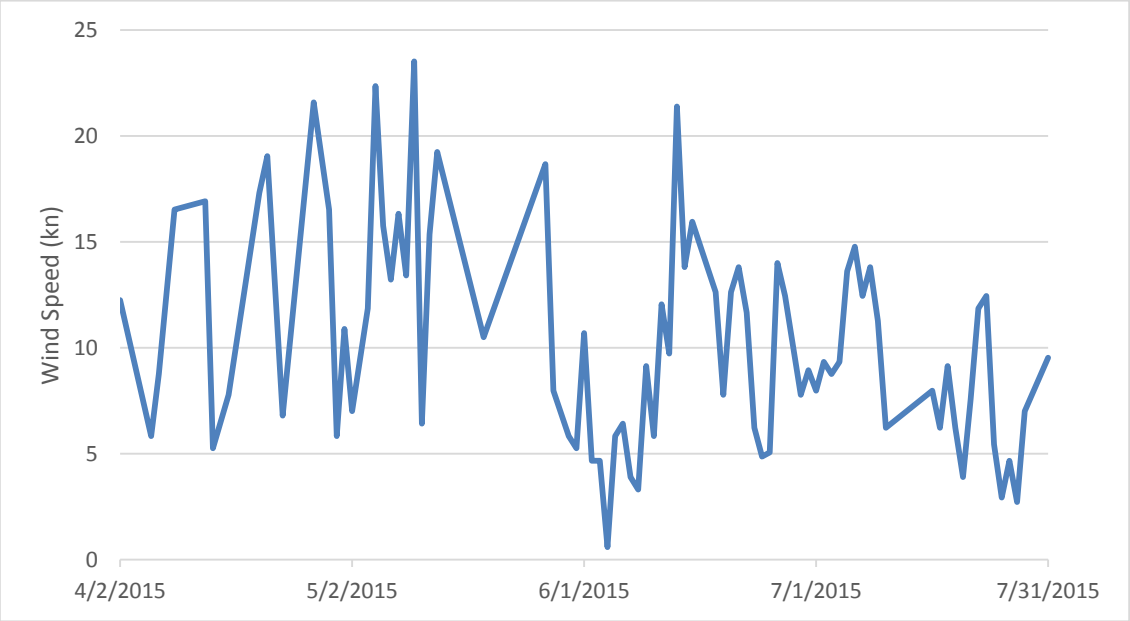

Figure 14 Wind speed (Kn) at sampling time. Data taken from NOAA's Pier 21 Station.

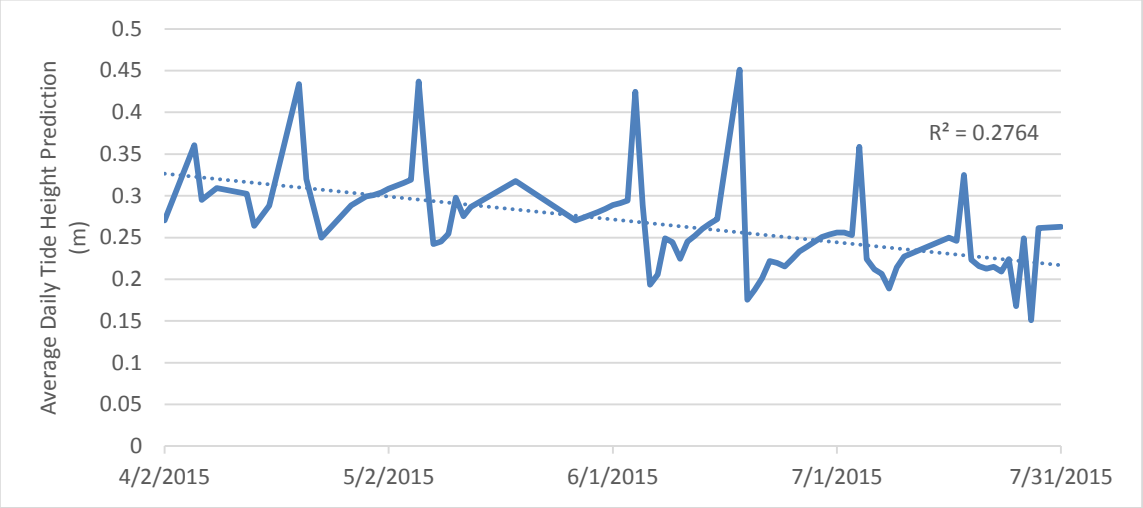

Figure 15 Average daily tide height prediction (m). Data taken from NOAA Galveston Bay Entrance station.

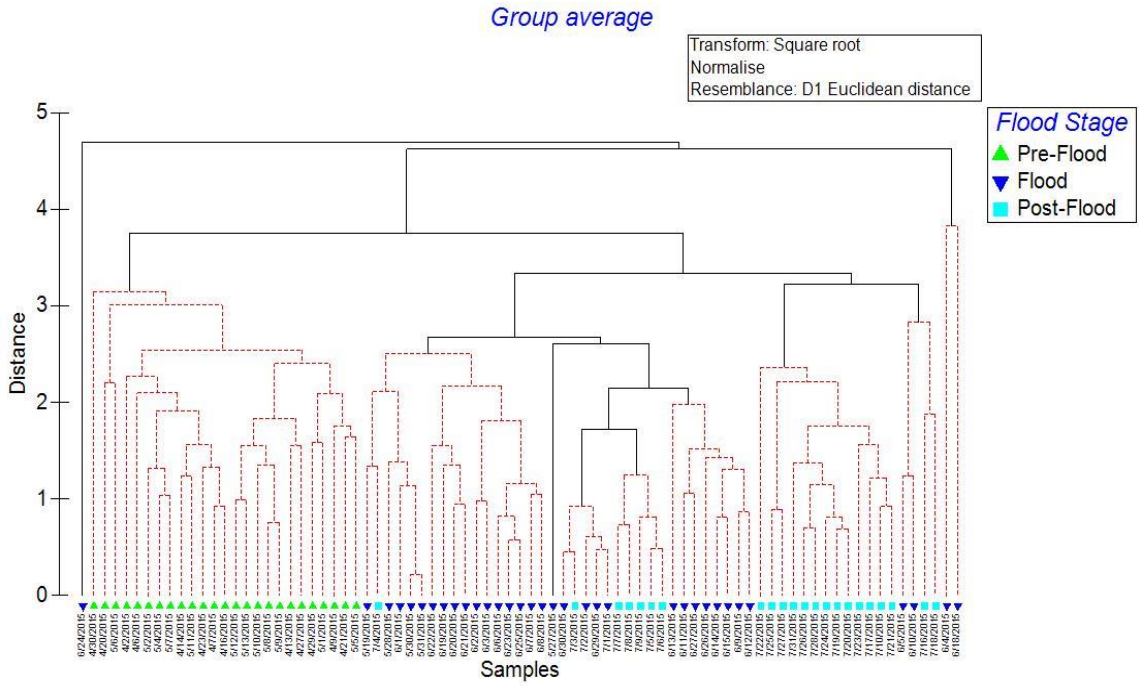

Figure 16 CLUSTER analysis of environmental data used to create the three flood stages.

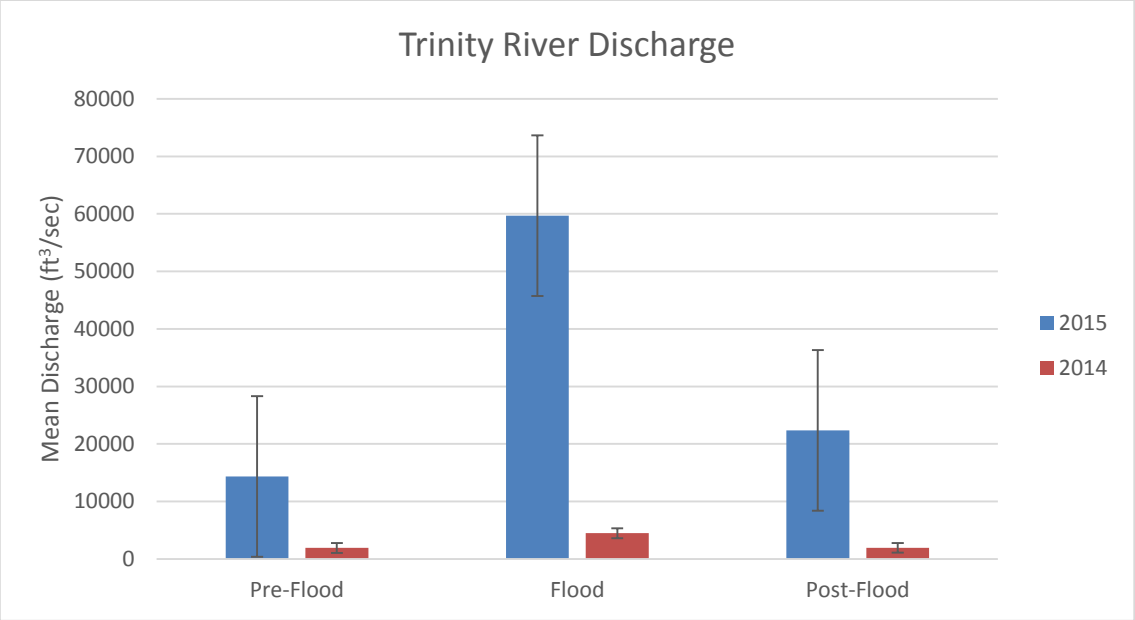

Figure 17 Mean discharge from the Trinity River during 2014 and 2015. Data taken from USGS Romayor Station.

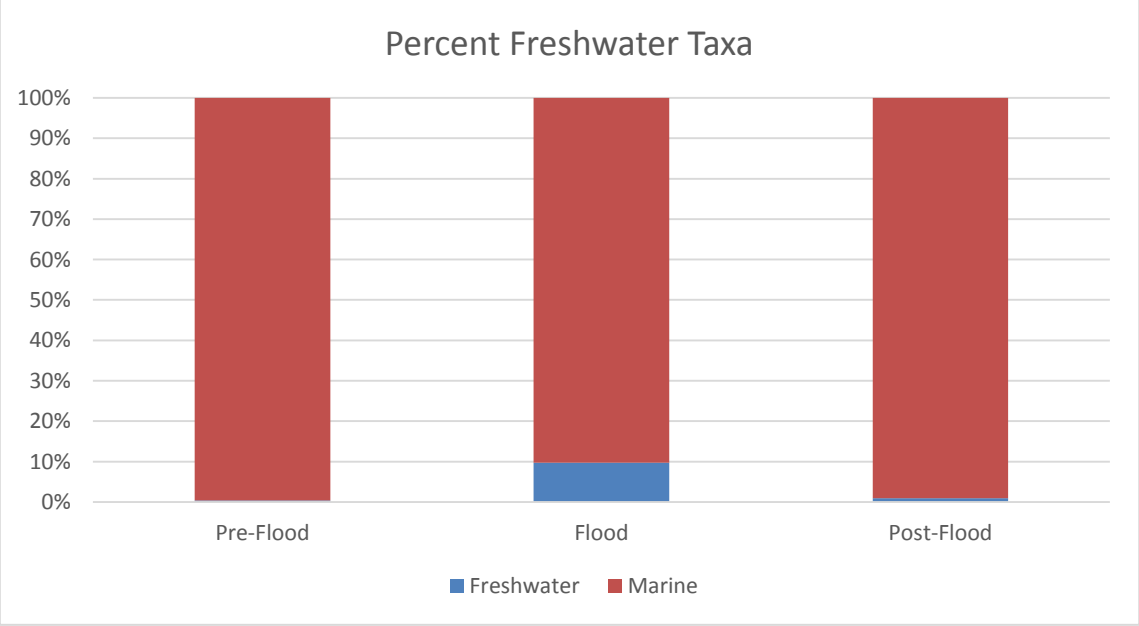

Figure 18 100 percent bar graph showing the percent of freshwater taxa abundance during each flood stage at the IFCB sampling station.

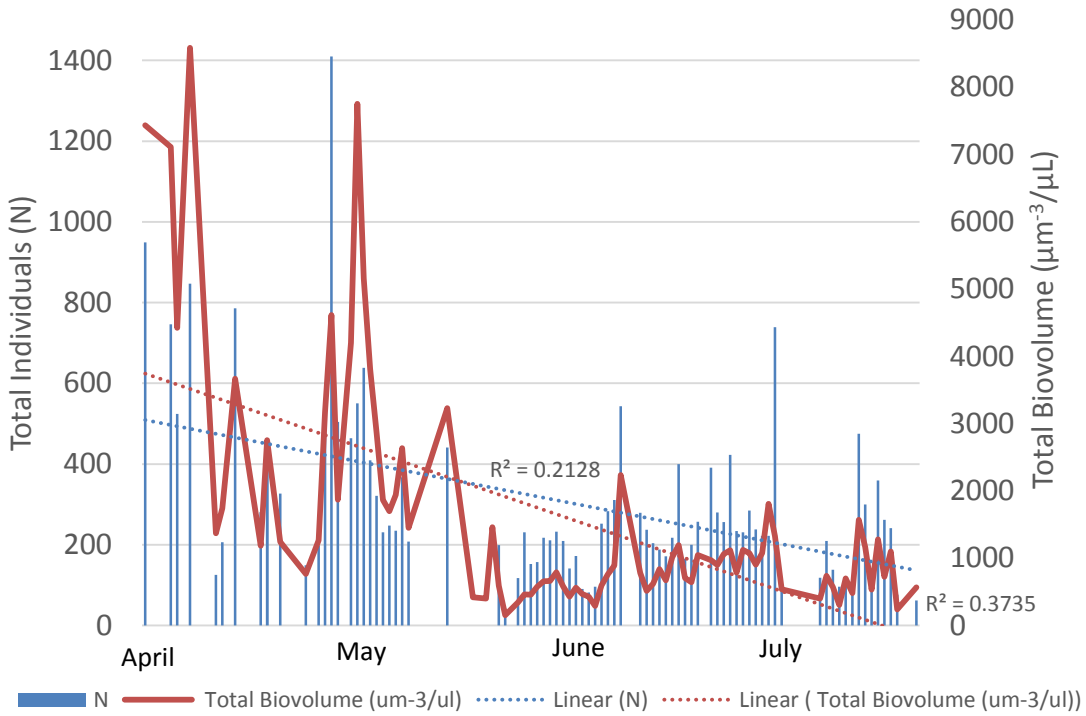

Figure 19 Total number of individuals and total phytoplankton biovolume for each sample at the IFCB sampling station.

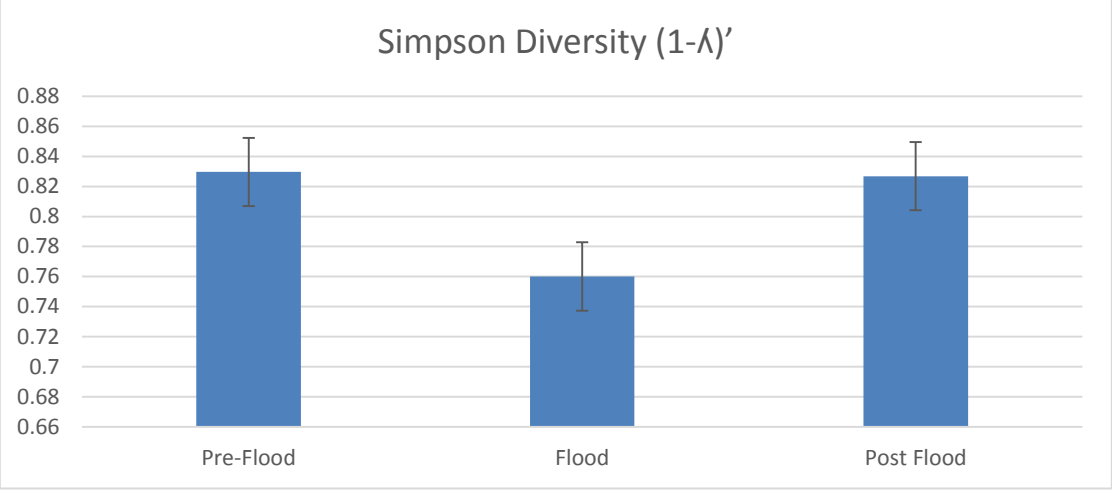

Figure 20 Simpson's diversity (1-ʎ)'of the phytoplankton genera at the IFCB station during each flood stage

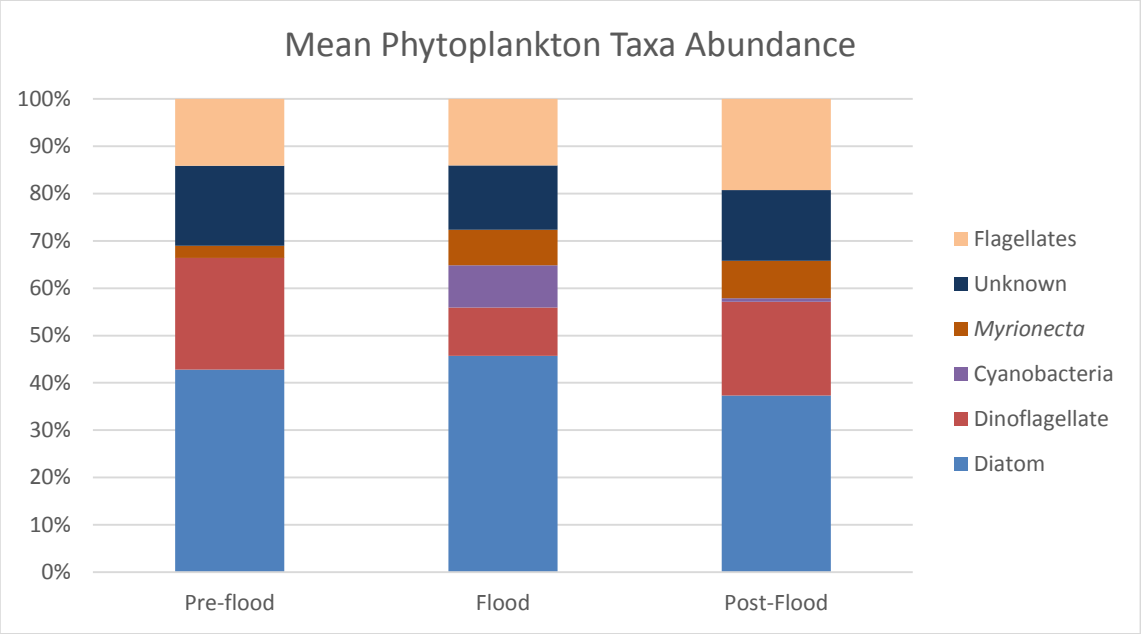

Figure 21 Mean abundance of the most common phytoplankton taxa during each flood stage.

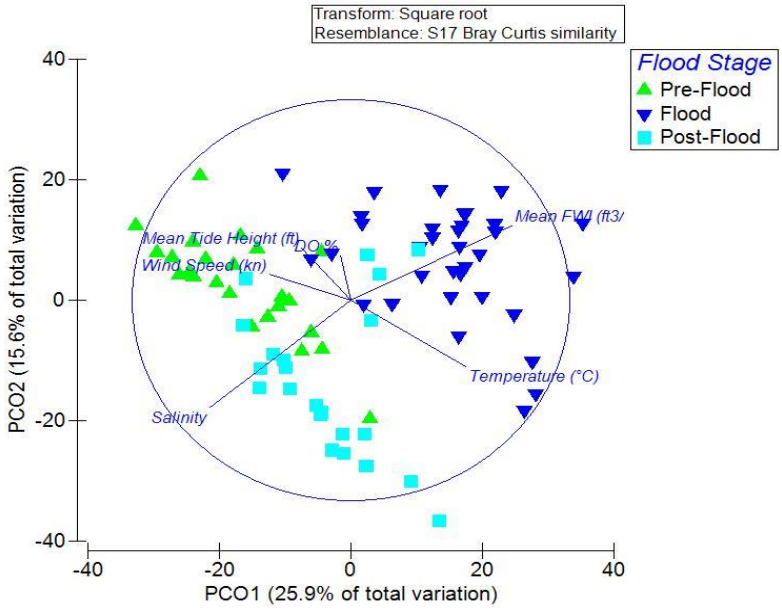

Figure 22 Principal coordinates analysis of phytoplankton community composition data overlaid with Spearman correlation vectors of environmental data.

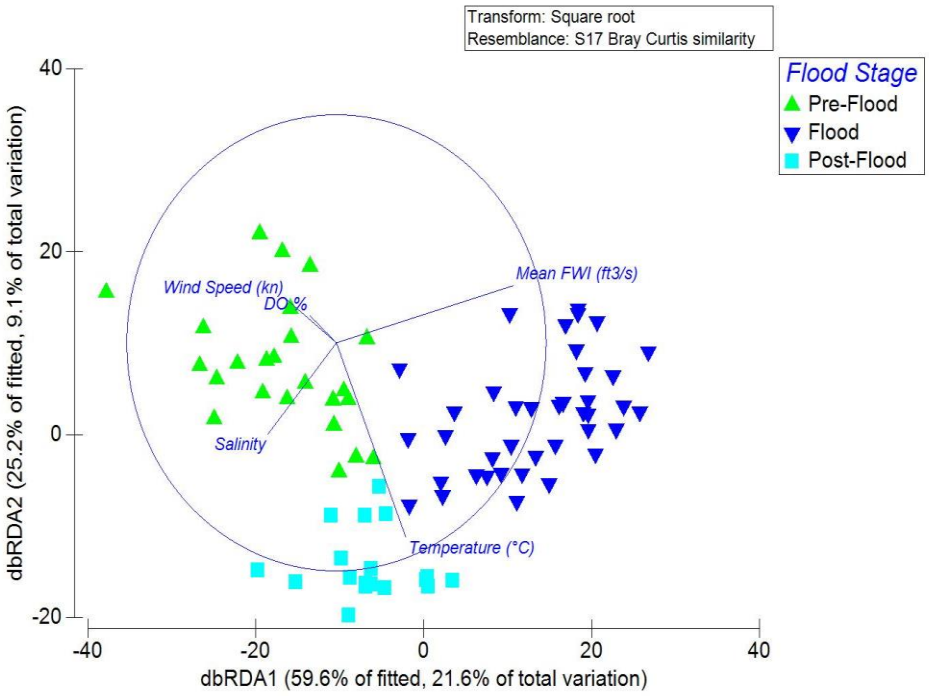

Figure 23 dbRDA plot of model associated with comparing the similarities of the community composition samples to environmental predictor variables.

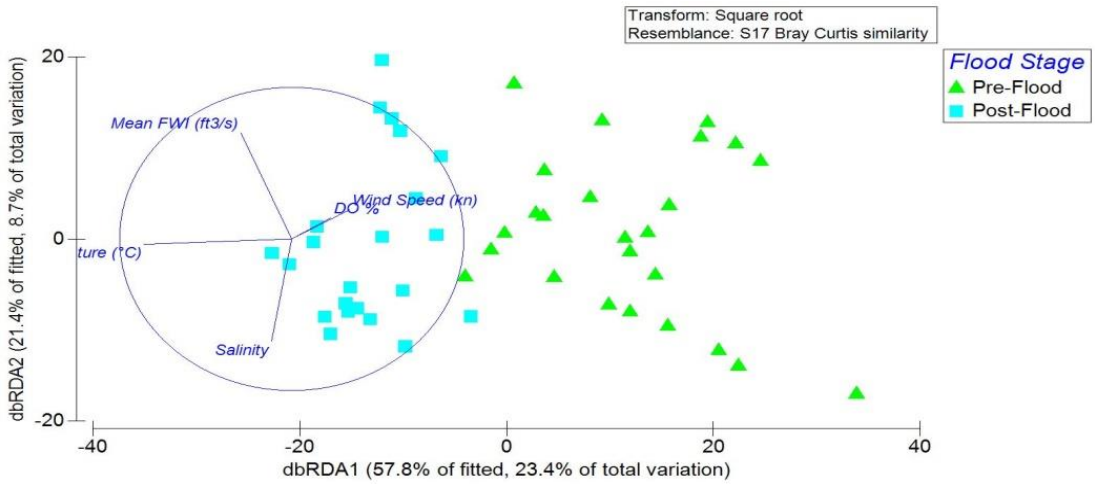

Figure 24 dbRDA of pre-flood and post-flood phytoplankton community composition data used to verify the DistLM used to explain the variation between the two flood stages.

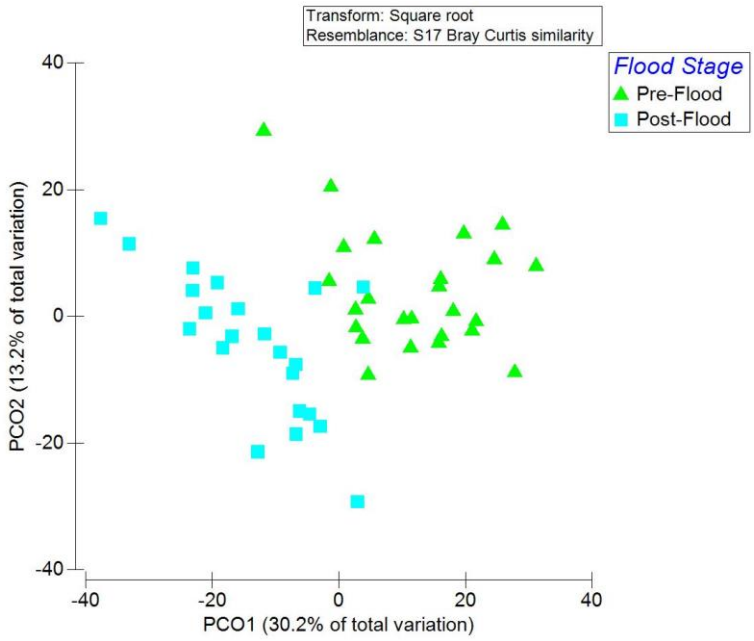

Figure 25 PCO of pre-flood and post-flood phytoplankton community composition data used to verify the dbRDA.

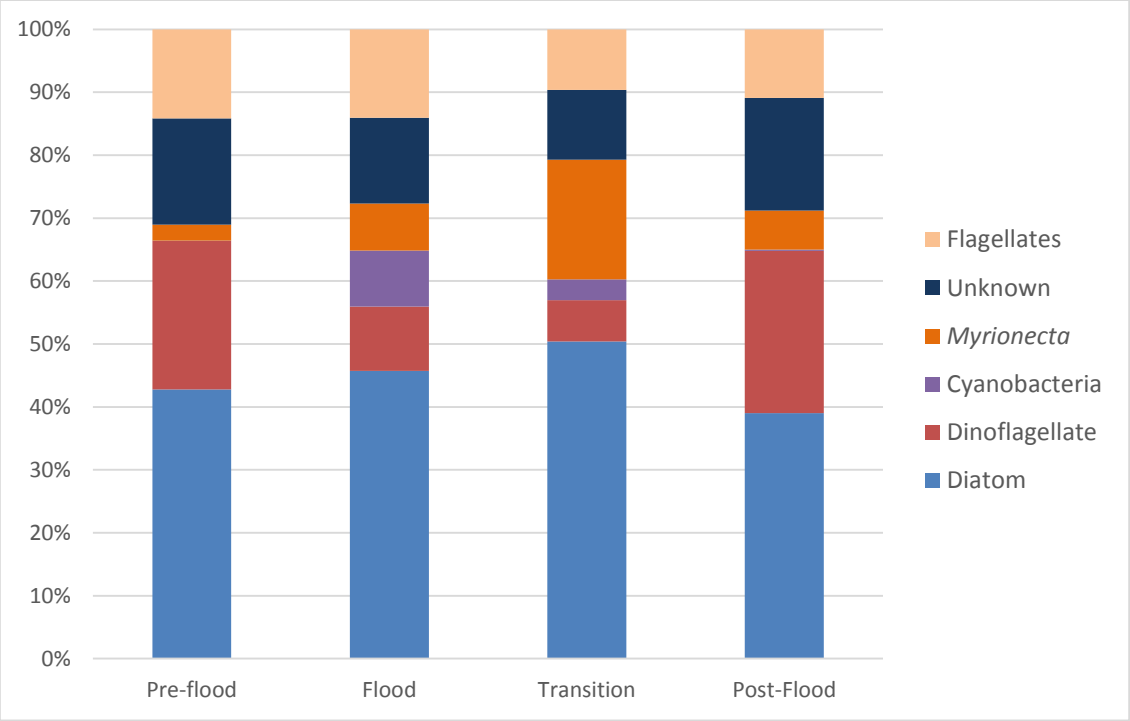

Figure 26 100 percent bar graph of most abundant taxa showing transition stage that was found using the PCO.

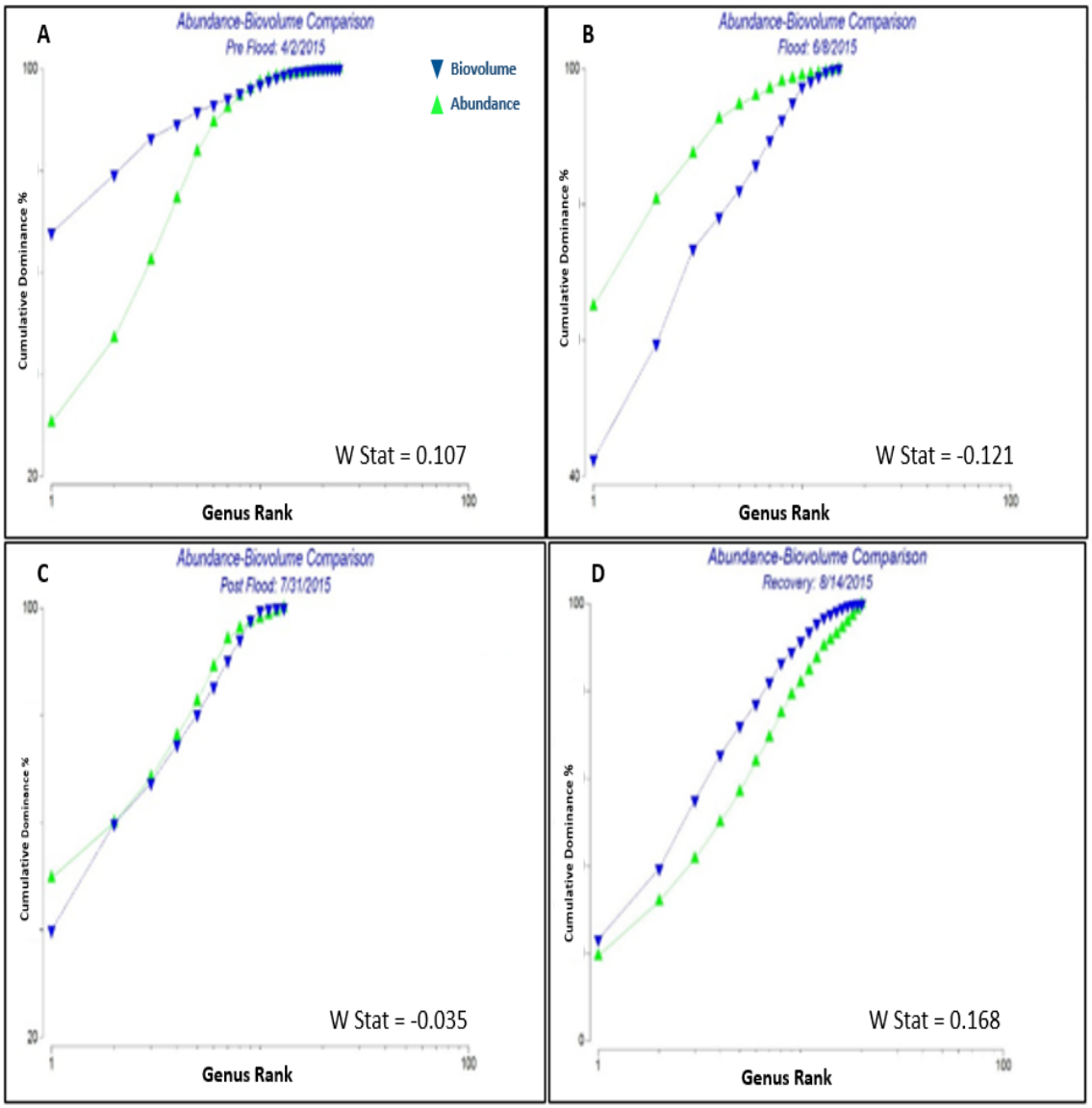

Figure 27 Series of abundance-biovolume comparison curves and their corresponding W-statistic that show the change in community size structure over the study period.

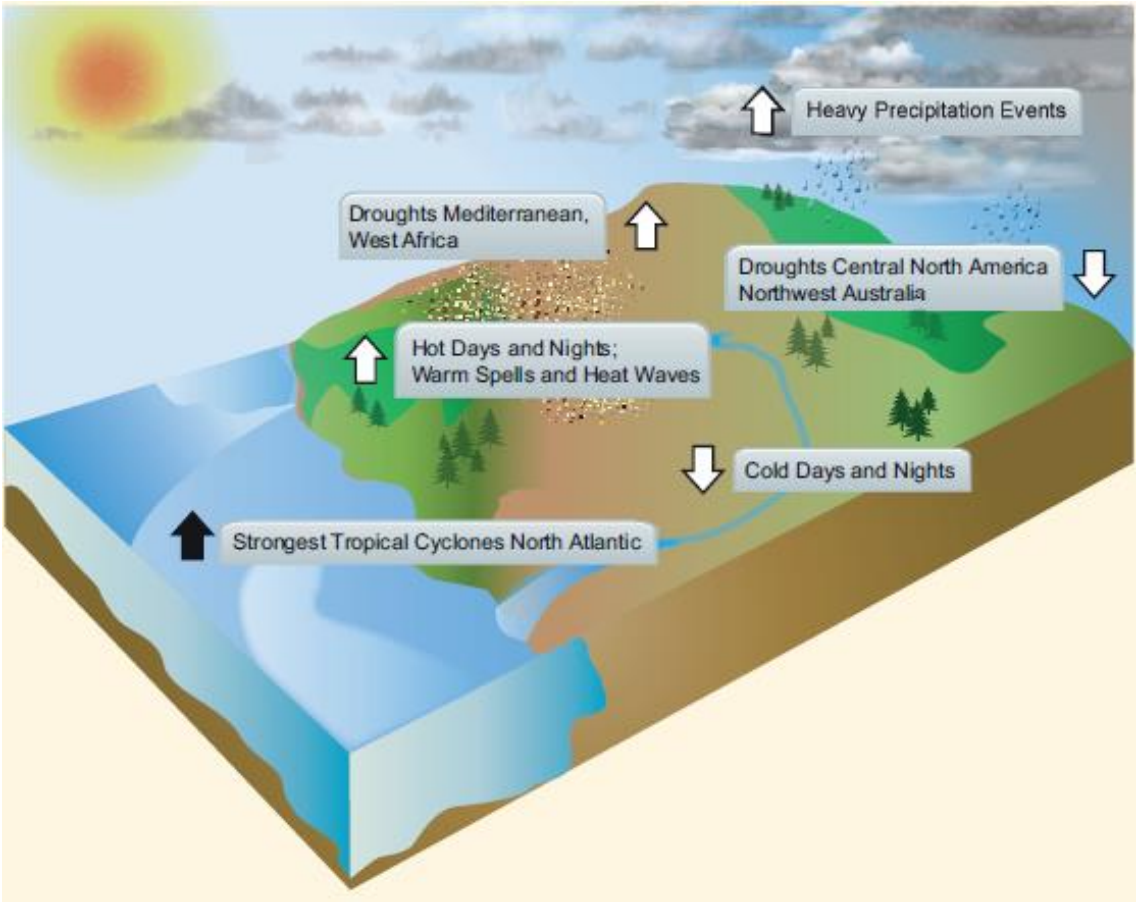

Figure 28 Trends in the frequency of climate events since the mid-20th century. Arrows indicate sign of change. Taken from 2013 IPCC report: Chapter 2: Hartmann et al., 2013.

APPENDIX B: TABLES

Table 1 Pre-flood, flood and post-flood stage dates for the 2015 extreme flooding event.

Flood Stage	**Begin**	**End**
Pre-Flood	4/2	5/13
Flood	5/19	7/2
Post-Flood	7/3	7/31

Table 2 List of Phytoplankton Taxa seen during study period at IFCB station. Includes number of genera and total number of groups for each taxa

Taxa	**Total Groups**	**# of Genera**
Diatom	31	28
Dinoflagellate	20	19
Cyanobacteria	4	3
Chlorophyte	4	4
Desmid	2	2
Xanthophyte	1	1
Dictyochophyceae	1	1
Phototrophic Ciliate	1	1
Flagellates	2	0
Unknown	2	0

Table 3 List of phytoplankton genera recorded during study period at IFCB station

Diatom	**Dinoflagellate**	**Desmid**
Bacteriastrum	*Akashiwo*	*Closterium*
Chaetoceros	*Alexandrium*	*Staurastrum*
Corethron	*Brachidinium*	**Xanthophyte**
Coscinodiscus	*Ceratium*	*Centritractus*
Cylindrotheca	Dinoflagellate Mix	**Haptophyte**
Cymatosira	*Dinophysis*	*Coccolithophore*
Ditylum	*Gonyaulax*	**Dictyochophyceae**
Entomoneis	*Gyrodinium*	*Dictyocha*
Eucampia	*Heterocapsa*	**Phototrophic Ciliate**
Guinardia	*Karenia*	*Myrionecta*
Helicotheca	*Katodinium*	**Flagellates**
Hemiaululs	*Noctiluca*	Euglenoids
Leptocylindrus	*Oxyphysis*	Flagellate Mix
Licomorpha	*Polykrikos*	**Unknown**
Lioloma	*Prorocentrum*	Colonial Round
Melosira	*Protoperidinium*	Round Mix
Meuniera	*Scrippsiella*	
Nitzchia	*Spatulodinium*	
Odontella	*Spiraulax*	

Table 3 Continued

Diatom	**Dinoflagellate**	
Paralia	*Torodinium*	
Pennate Diatoms	**Cyanobacteria**	
Sigmoid Pennates	*Anabaena*	
Pseudo-nitzschia	Elongated filamentous	
Pseudosolenia	*Merismopedia*	
Rhizosolenia	*Trichodesmium*	
Rodlike Diatoms	**Chlorophyte**	
Skeletonema	*Oltmannsiellopsis*	
Striatella	*Pediastrum*	
Thalassionema	*Pyramimonas*	
Thalassiosira	*Scenedesmus*	
Triceratium		